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ABSTRACT

"Science as a Way of Knowing" is a project of the education committee of the American Society of Zoologists and 11 other organizations designed to offer suggestions for making the teaching of biology at the college and university level more effective. Each year the project focuses on an important subfield of biology and: (1) sponsors a symposium on the topic area; (2) develops a film program; (3) publishes an essay with an extensive bibliography; and (4) publishes the symposium proceedings. The proceedings of the 1985 symposium on human ecology are presented in this document. Articles included are: "Science as a Way of Knowing--Human Ecology: Opening Remarks" and "Science as a Way of Knowing--Human Ecology" (John A. Moore); "Human Ecology for Introductory Biology Courses: An Overview" (Paul R. Ehrlich); "The Human Population: Size and Dynamics" (Anne H. Ehrlich); "Science as a Way of Knowing: Man and Food" (John L. Fischer); "On the Trail of Atmospheric Mutagens and Carcinogens: A Combined Chemical/Microbiological Approach" (James N. Pitts, Jr.); "Trends in Health-Ecological Consequences for the Human Population" (Lester Breslow); "Ecological Aspects of Disease and Human Populations" (Robert M. May); "Man and the Sea-The Ecological Challenge" (G. Carleton Ray); "Human Ecology: The Subsersive, Conservative Science" (Garrett Hardin); and "Films and Videotapes in Human Ecology" (Gary Anderson and Nathan H. Hart). (JN)

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SCIENCE AS A WAY OF KNOWING
II—HUMAN ECOLOGY

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II

SCIENCE AS A WAY OF KNOWING—HUMAN ECOLOGY

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AMER. ZOOL., 25:377–378 (1985)

Science as a Way of Knowing—Human Ecology Opening Remarks

JOHN A. MOORE

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We now begin the second annual session of *Science as a Way of Knowing*, a project of the Education Committee of the American Society of Zoologists and eleven other organizations.

The goal of *Science as a Way of Knowing* is to offer suggestions for making the teaching of biology at the college and university levels more effective. Each year the project considers an important subfield of biology. Last year it was Evolutionary Biology and this year it is Human Ecology. Next year at the Baltimore meeting it will be Genetics and at the Nashville meeting in 1986 we will focus on Developmental Biology.

Our package consists of four parts. Each year there will be: first, a symposium where outstanding scientists develop various aspects of the year's topic; second, a film program; third, a published essay with an extensive bibliography; and fourth, the publication of the entire proceedings in the *American Zoologist* followed by the wide distribution of reprints throughout the world.

These activities are made possible by a grant from the Carnegie Corporation of New York. The Corporation is not responsible for what we say but its generosity makes it possible for us to say it. We could not have a more understanding patron.

The three main themes of the *Science as a Way of Knowing* project are

1. to emphasize the procedures that enable us to understand the natural world,
2. to show how these understandings can be united in conceptual schemes that carry understanding to a higher intellectual level, and
3. to explore how the data and procedures of science can serve as powerful adjuncts to achieving human goals that rest on humane decisions.

There is no branch of science that is more human oriented and more relevant than Human Ecology. All human history is but a reflection of the workings of ecological principles. What we are and what we will become depends, absolutely, on our interactions with the living and non-living environments. Nevertheless, Human Ecology tends to be given short shrift in many university courses in biology. I ask you now to consider whether or not this can be justified.

We like to assume that higher education is effective in preparing the maturing generation for life in that real world where disciplined and informed minds must deal with the difficult problems of the day—many of which are life threatening. Is that the usual outcome of higher education? Surely to some extent, but I cannot escape the feeling that for most of the pressing problems of the day we are not producing an effective cohort with those informed and disciplined minds. We must reach this conclusion since there are overwhelming data to indicate that in many parts of the world human activities are rendering the natural world ever less able to provide the resources and conditions required for human life. Students may learn a very great deal but does this include the information, the perspectives, and the philosophical stance to deal with such matters?

Consider the following. Front line news across the nation today is the terrible famine in much of Africa, especially Ethiopia. You can conduct an interesting and sobering experiment by asking students and peers what should be the proper course of action for the United States and other nations in a position to help. The usual analysis that I find is that "Hungry people

[1] From the Symposium on *Science as a Way of Knowing—Human Ecology* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1984, at Denver, Colorado.

need food and so the thing to do is feed them." It hardly takes a university education to achieve that level of sophistication. I have yet to hear a person say, "The real problem is how can we prevent such happenings."

Possibly the first question should be reworded to ask, "What would be the most humane action in the long run?" In my small sample no one seems to have considered this aspect of the tragedy. The decisions that are being made nearly always deal with the problems of today—not of long term solutions. It is far from simple to reach a decision on what *is* the most humane solution to endemic famine or to the many other seemingly intractable problems of Human Ecology, yet decisions must be made.

Many years ago I found myself in a plane sitting next to Marston Bates, the distinguished naturalist, author, and malaria specialist. He had been recalled by the Rockefeller Foundation from his laboratory in Villavicencio (Colombia) to return to headquarters and *think*. The Foundation had become increasingly uneasy about its worldwide programs in public health. Not that the programs were failing—they were often a spectacular success. But could it be that these programs were keeping people free from disease only that they would die later of starvation? That was what Marston was to think about and he had come to believe that more food was of greater importance than more health. The Foundation soon changed its projects and some of them gave us the "Green Revolution." I asked Marston about the obvious risk of saving people from starving now with the probable consequence that more would starve later. His answer was, "The next generation will have to deal with that one."

We are that generation. Unless we have the courage to make some of the most heart-breaking decisions ever faced by human beings, we will be compromising the future of humanity. There is little evidence that our leaders have the knowledge, courage, or deep humanity to make such decisions. Science alone cannot decide what is "right"—that is a human decision. Yet the data and concepts of Human Ecology are fundamental in guiding us toward humane decisions. I cannot escape the feeling that, to the extent that we fail to prepare students to deal with these problems, we fail as individuals and as a profession. Biologists must play their essential role as interpreters of the present and as guides to the future—if there is to be an acceptable future.

The unifying characteristic of the individuals who are speaking at this symposium is that they are scientists who have been preeminent in their use of science for the betterment of humanity. To varying degrees they have left the relative ease and security of the laboratory bench to deal with ignorance, intolerance, greed, apathy, selfishness, and undisciplined emotion. They have emphasized that the overriding goal of humanity can no longer be the conquest of nature because, to the degree we conquer nature, we defeat ourselves. Unless we join them by working effectively in our classrooms, the human future is bleak indeed. That future may or may not see a Nuclear Winter but, if we continue to flaunt the laws of nature, surely there will be an Ecological Winter.

But never forget for one moment that we have the knowledge and power to prevent that future. Our profession must transmit that fact and hope.

AMER. ZOOL., 25:379–394 (1985)

Human Ecology for Introductory Biology Courses: An Overview[1]

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SYNOPSIS. Human ecology, specifically the population–resource–environment dilemma, should be given thorough coverage in every introductory biology course. To aid educators in integrating it into the course, the subject is outlined here and suggestions are given on what topics should be emphasized and how they might be introduced to students. Special attention is given to the fundamental role of population growth in the dilemma, and to the complex interactions among population growth, depletion of resources, and environmental deterioration. Today's human population size appears to be above the long-term carrying capacity of Earth, and is only maintained (albeit often badly) by the exploitation of a "one-time bonanza" of fertile soils, fossil fuels, concentrated ores, ground water, and other species of organisms. If current trends continue, the depletion of these resources will progressively degrade the human environment, destroying the capacity of natural ecosystems to supply civilization with indispensible services. The results will be in increasing frequency and severity of disasters, especially famines, that will at first most seriously affect the poor. But the rich will increasingly be impoverished, and be engulfed also. The basic solution to the dilemma is reduction of the size of the human population to one well below the long-term carrying capacity (one living on resource "income" rather than "capital") and establishing an equitable society with a sustainable economic system.

INTRODUCTION

In its broadest definition, human ecology would deal with all interactions between human beings and between each person and his or her environment. It would subsume virtually the entire body of human knowledge, including history, languages, accounting, engineering, and so on. Such a broad definition, however, obviously cannot form the basis of a coherent discipline. Therefore human ecology has normally focused (*e.g.*, Ehrlich and Ehrlich, 1970) on four main areas:

1. The dynamics of human populations;
2. The use of resources by human beings;
3. The impact of human beings on their environment;
4. The complex interactions among 1–3.

Finding ways to ameliorate the increasingly serious consequences of events in these four areas I will call the human dilemma. It has also been called the human predicament or world problematique (Meadows *et al.*, 1972). The dilemma represents the greatest challenge ever faced by *Homo sapiens*—the survival of civilization is certainly at stake; the survival of our species may be. The biological sciences provide all-important insights into the dilemma, and it should therefore receive substantial coverage in introductory biology courses. Even narrowly defined, however, human ecology is such a vast topic (Ehrlich *et al.*, 1977) that its treatment must be abbreviated. Fortunately, however, many basic biological concepts can be illustrated with material from human ecology, often permitting an instructor to kill two birds with one stone as he or she integrates human ecology into the course.

I would now like to examine what every informed citizen should know about each of the four areas. I believe that this is the best criterion for determining what should be included in an introductory course, since there is no other place in the educational system where a student is likely to be exposed to this crucial material.

POPULATION

Few topics are more thoroughly misunderstood by the public, including college students *and* faculty, than the dynamics of the human population and its significance to other issues in human ecology. Most people do not know the current size of the

[1] From the Symposium on *Science as a Way of Knowing—Human Ecology* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1984, at Denver, Colorado.

human population, its current growth rate, or anything of the history of human population growth.

Basic demography

The treatment of human ecology should briefly deal with the elements of historical demography, today's population statistics, and the definition of crude death and birth rates, growth rates, fertility rates, and the net reproductive rate (Ehrlich *et al.*, 1977; A. Ehrlich, 1985). The latter is important for understanding the momentum of population growth. It is therefore also crucial to interpreting various kinds of population projections and to grasping why efforts to control population growth and size will ordinarily progress very slowly. Treatment of these subjects does not require mathematics beyond arithmetic, but explaining the net reproductive rate must be done with care—perhaps the basic idea is best approached by first discussing the total fertility rate. These and related topics are covered in another paper in this symposium (A. Ehrlich, 1985). All of these subjects can be integrated into a more general treatment of population dynamics, and the similarity of the processes in human beings to those in other animals with overlapping generations can be pointed out.

Two other population-related topics deserve careful attention. One is the preoccupation of demographers (as opposed to ecologists) with changes in birth rates as opposed to changes in death rates. For example, demographic projections standardly assume that age-specific mortality rates will either remain constant or move lower. But these rates can also rise, as is obvious from both first principles and the occurrence of increases in various areas in the last decade (Gwatkin, 1980; Newland, 1981) and right now in parts of Africa. Ignoring death rate rises tends to create for the student the comforting illusion that humanity has somehow utterly freed itself from Malthusian constraints.

Ideally, the connection between environmental factors and changing trends in death rates in less-developed countries should be made. Early progress in reducing them was dramatic as the parasitic and communicable diseases rather easily controlled by Western medical technology were conquered. But the "great killers of children—diarrhea, pneumonia, malnutrition—are beyond the reach of [that technology]" (Bryant, 1969). Supplying pure water and adequate diets for ever-increasing populations in poor nations can be extremely difficult, requiring a level of economic progress and political organization that is often wanting. And the prospects of a return of high mortality from parasitic and communicable diseases always lurks in the background—underlined by a resurgence of malaria in many areas.

Carrying capacity

The second topic is that of the definition of overpopulation and the related notion of carrying capacity—the number of people that can be supported by a given habitat, or in this case, the entire planet. One often hears it said that the world is not overpopulated with human beings. Various reasons are given: because there is lots of empty space in Nevada; or because, if the economic system were different or if people were saintly and willing to share their food equally (or some such), everybody would have enough to eat; or because people themselves are the "ultimate resource," and greater numbers of brains could help to solve all of humanity's problems (Simon, 1981).

Most of those holding the "no overpopulation" view compound a number of elementary errors. These include the notion that space itself is a critical limiting resource for *Homo sapiens* today; that adequacy of the contemporary food supply is the only measure of carrying capacity; that there is a strong positive correlation between population size and technological innovation; that carrying capacity is a constant; and that it is only today's carrying capacity that counts.

Of course, space itself does not limit the human population and will not in the foreseeable future. People in relation to space is not the crucial issue; it is people in relation to resources (not just food resources) and the capacity of environmental systems to support human beings. Furthermore, it

is quite clear from a simple examination of the world today that brute numbers are no guarantee of technological innovation. Abundant resources, appropriate educational traditions, a democratic government, and a relatively free market economic system seem much more likely to be determining factors.

A fundamental point is that *carrying capacity has to be determined on the basis of the kind of animals that are occupying the habitat.* A meat-eating, warlike people whose economic system is based on gross inequities would (everything else being equal) exceed the carrying capacity of its environment sooner than a population of largely vegetarian, peaceful, equally sharing human beings. Students should be told that, in theory, a population could move above or below the carrying capacity while not changing in size, but by changing its behavior. A conservative population policy would be designed to limit the meat-eating population, which closely resembles today's *Homo sapiens*, to a size that could be comfortably supported—sustained so that even those at the bottom of the economic ladder would be adequately cared for. A radical population policy, in contrast, would ignore approaching limits on the basis of an expected transformation of today's human behavior into a more saintly pattern.

It is not clear, however, that today's human population would be below the long-term carrying capacity even if it were made up of saints. In order to be below that carrying capacity, the population should not be degrading the ability of the planet to support people in the future. But, as we will see, that is precisely what it *is* doing. Perhaps the most important point of all for a student of human ecology to understand is that our species is now *living on its capital*—a one-time resource bonanza that will not be replaced on a time scale of interest to society.

RESOURCES

Human beings, of course, use a wide variety of resources. Perhaps the most basic of these is food; and (especially in industrialized societies) various other resources such as fresh water, fertile soils, fossil fuels, and many minerals are deeply involved in the production of crops. Food production therefore provides an obvious focus for a discussion of the broader topic of resources.

Food production

As with the basics of population growth, the basics of how human societies produce and distribute their food are largely unknown to college students. In addition to presenting an overview of food production past and present, several points should be emphasized to biology students.

First, agriculture, because of its dependence upon sunlight for photosynthesis, is and will remain a highly dispersed enterprise. This means that transport is an essential feature of any non-subsistence agricultural system. Not only must agricultural products be moved from farms to consumers, but inputs such as seeds, fertilizers, pesticides, and so on must be moved to the farms.

Second, in spite of a widespread myth to the contrary, modern agriculture remains highly dependent on the vagaries of weather. Appropriate temperatures and, in non-irrigated areas, appropriate amounts of rainfall are critical to yields (Schneider and Londer, 1984). And irrigation is only a partial (usually expensive and often temporary) solution to the problems of inadequate moisture.

Third, agricultural productivity is heavily dependent, and will continue to be dependent, upon soil quality.

Fourth, the success of high-yield agriculture is basically a result of the efforts of plant geneticists, *not* of the production of synthetic pesticides and artificial fertilizers, although the latter are important concomitants.

And fifth, the sociology, politics, and especially the *economics* of agriculture and food distribution are all crucial determinants of how many human beings can be adequately fed at a given time and place.

The treatment of agriculture should be ecological and evolutionary in focus. The properties of agroecosystems should be developed as an extension of the treatment of natural ecosystems—and should include a discussion of the problems of arresting

succession and controlling organisms that compete with *Homo sapiens* for the primary production of the system. Here is a good place to introduce the topic of pesticides (van den Bosch, 1978; Perkins, 1982), the evolution of resistance to them, and coverage of the population dynamic and genetic reasons that predators are more likely to be decimated by broadcast spraying than are herbivores (Ehrlich *et al.*, 1977). The last topic can be briefly tied to the problem of bacterial resistance to antibiotics. A great many fundamental evolutionary and ecological issues such as plant-herbivore coevolution, sibling species, competition, and predation, can be dealt with in a context of integrated pest management (*e.g.*, Ehrlich and Ehrlich, 1978; Richardson, 1978; Flint and van den Bosch, 1981).

Energy and minerals

Energy and minerals will necessarily have to be given relatively short shrift within an introductory biology course. It should be pointed out to students that the sun is and always has been the basic energy source for *Homo sapiens*. That fossil fuels are stored solar energy, originally captured by photosynthesis, should be emphasized, as should the dependence of many people on firewood as an energy source (Postel, 1984) and the basic role of the sun in the production of hydroelectric power. They should be told that nuclear power is the only significant exception to the solar-origin-of-energy rule.

The principal advantages (A) and disadvantages (D) of various energy technologies can be touched on (Holdren, 1976; Ehrlich *et al.*, 1977): fossil fuels (A—convenience of portable fuels; D—atmospheric buildup of CO_2, acid rains, direct health risks from air pollution); nuclear fission power (A—avoids most fossil fuel hazards, supply potentially much greater; D—proliferation of nuclear weapons, chance of catastrophic accident, problems of radioactive waste disposal); hydroelectric (A—clean, not dependent on fuel supply; D—floods land, temporary because dams silt up); biomass (A—available where fossil fuels are scarce, potentially renewable; D—same as fossil fuels in many applications, competes for land with agriculture, can create similar environmental problems).

The most critical thing, however, that students must learn about the ecology of energy used by human beings is that it is not inadequacies of supply that place the major constraints on energy use, but rather the inevitable environmental consequences of that use (Gleick and Holdren, 1981). These consequences also place the most important limits on the mobilization of materials. Some mineral resources could be extracted in quantity from very low concentrations in common rock or sea water—*if* humanity could afford the energy (it might) and *if* it could avoid unacceptable environmental deterioration (it could not). This is a good place to show students the practical consequences of the second law of thermodynamics—the importance of the *concentrated* mineral deposits that humanity inherited and the inevitability of creating heat pollution at the very least as a consequence of using energy to concentrate dispersed minerals as the richest deposits of ores are depleted.

Fresh water

Fresh water is a resource that students are usually taught is renewable. It is therefore very important to stress that in many ways it is nonrenewable. Mention should be made of the dependence of our society and others on ground water, and of the disparity between rates of withdrawal and rates of recharge in aquifers like the Ogallala. Other problems include the collapse of overpumped aquifers and the intrusion of salt water into them; the paving over of recharge areas; and the pollution of ground water by plumes from toxic-waste disposal sites (as well as the extremely slow rates of self-purification of water under ground).

Soils

Deep, rich agricultural soils are another resource whose non-renewability on a time scale of interest to society is not widely understood. Soils are usually generated at a rate of inches per millennium; they are being eroded away in many areas in rates of inches per decade or even faster. It is

crucial that people understand that soil is not just ground-up rock, but an extraordinarily complex ecological system that is totally dependent upon its flora and fauna for its fertility (Jenny, 1980; Ehrlich and Ehrlich, 1981). Depletion of soils, may, indeed, be the most serious problem with nonrenewable resources in the next fifty years or so. All people should pay heed to the warning of Lester Brown (1981, p. 13): "Civilization can survive the exhaustion of oil reserves, but not the continuing wholesale loss of topsoil."

Organic diversity

The least recognized, but in the long run unquestionably most important, depletion of a nonrenewable resource is the accelerating attrition of organic diversity (Raven, 1978; Myers, 1979, 1984; Ehrlich and Ehrlich, 1981). The principal cause of extinctions today is the outright destruction of habitat by humanity, reinforced by the growing toxification of the planet and the direct endangering of organisms of economic importance. Students should have been introduced to basic evolutionary theory *before* this topic is covered. The claim is sometimes made (Witchell, 1974; Simon and Wildavsky, 1984) that one need not be concerned about the current extinction epidemic because past extinctions were not harmful to humanity. Simon and Wildavsky managed to put forth this notion in a perfect example of a "spherically senseless" statement (one that is absurd from any viewpoint): "If genetic extinction doomed mankind, presumably it would have died a billion deaths by now!" Needless to say, the history of extinctions (including the absence of *Homo sapiens* at the time of past catastrophic episodes, so that people did not suffer their consequences) and today's rapidly changing relationship between *rates* of speciation and extinction should be covered.

Current estimates indicate that as many as 50 percent of all the species of plants, animals, and microorganisms on the planet could become extinct in the next four or five decades, largely as a result of the clearing of tropical moist forests (Raven, 1976; Myers, 1983, 1984). And an equally important attrition of natural populations is proceeding at an even higher rate.

In the eyes of many, this loss of diversity will be a great ethical and esthetic catastrophe (Ehrenfeld, 1978; Ehrlich and Ehrlich, 1981). Biology students in introductory courses should be introduced to this ethical issue, perhaps in conjunction with the growing debate on animal experimentation (Moss, 1984; Ritvo, 1984). The loss of biotic diversity unquestionably will also have enormous direct economic consequences—among other things, denying humanity access to many potential foods, medicines, industrial products, and energy sources (Myers, 1979; Ehrlich and Ehrlich, 1981).

Ecosystem services

Serious as these impacts are, however, they will be dwarfed by the loss of ecosystem services that will follow as a consequence of the extinctions. Natural ecosystems provide an array of free "public services" without which civilization could not persist. These include maintenance of the quality of the atmosphere, amelioration of the climate, and the generation and preservation of the soils that are crucial to agriculture and forestry, control of the hydrological cycle, disposal of wastes, recycling of nutrients, provision of food from the sea, control of more than 95 percent of all the potential pests of crops and carriers of disease to human beings, and the maintenance of a vast "genetic library." Humanity has already withdrawn the very basis of civilization from that library, and its potential has barely been tapped (Holdren and Ehrlich, 1974; Ehrlich *et al.*, 1977; Ehrlich and Ehrlich, 1981). The 5–30 million (Erwin, 1982) species of other organisms are critical working parts of ecosystems. Extermination of populations and entire species has already impaired the delivery of some services in many areas, even though the rate of extinctions in the recent past has been trivial compared to those projected for the near future. And, in most cases, there is no way that human ingenuity can satisfactorily substitute for the services nature provides (Ehrlich and Mooney, 1983).

The discussion of most ecosystem services can be interwoven into the material already included in an introductory course on ecosystem structure and functioning. The provision of food from the sea can be dealt with under marine ecosystems (e.g., nutrient upwelling, role of estuaries), biogeography (location of major stocks; role of coral reef fisheries), and population ecology (dynamics of exploited populations).

It is essential that biology students understand that, both from the standpoints of the survival of other species and of the welfare of humanity, extinction of populations is just as important as extinction of species. Once most of the genetic variability is removed from a species by the extinction of most of its populations, its chances of survival are severely compromised (Frankel and Soule, 1981). At the same time, the possibility of such an impoverished species being developed as a resource for *Homo sapiens* and its value in helping to provide ecosystem services will both be very much reduced. Here again, the need for basic background in evolutionary theory is obvious.

The importance of ecosystem services and the role of organic diversity in supplying those services are among the least understood aspects of human ecology. Failure to comprehend this aspect of life on Earth is alone responsible for many of the common misperceptions of the population–resource–environment crisis that are discussed below.

ENVIRONMENT

The destruction of ecosystem services, the consequences of their loss, and what can be done to preserve them should be the framework for the discussion of environmental issues in any first-rate introduction to human ecology. Unfortunately, disproportionate attention usually is given instead to the direct effects on human beings (and their artifacts) of lowered air and water quality. Problems such as noise pollution, generation of mesothelioma by asbestos exposure, and even the health impacts of smog are relatively trivial in comparison with major threats faced by *Homo sapiens* as a whole (even though they can be extremely serious for the people directly affected). But by far the most serious environmental problems are those whose impacts on human society are indirect—mediated by the changes people wreak in ecological systems.

Major assaults on ecosystems

Perhaps topping off the list are those problems that have the potential for causing large scale changes in the climate. The buildup of carbon dioxide in the atmosphere, with its potential enhancement of the so-called greenhouse effect, is a phenomenon that could create havoc for civilization in a matter of decades (Revelle and Suess, 1957; Woodwell, 1978; Clark, 1982; NRC, 1983; Schneider and Londer, 1984). The disruption of agricultural production could lead to the deaths of as many as one billion people by starvation (Holdren, 1978)—a tragedy perhaps foreshadowed by the ecocatastrophe in Africa that is being witnessed via television today.

Only slightly less threatening than the CO_2 buildup is the menace of acid precipitation (Likens *et al.*, 1979; EPA, 1980; Brimblecombe and Stedman, 1982; Tonnesson and Harte, 1982; Pearce, 1982; Harte, 1983; Havas *et al.*, 1984; Schneider and Londer, 1984). There is no serious scientific dispute that the acids are anthropogenic, or that they have already devastated aquatic ecosystems in various parts of North America and northern Europe, with serious economic consequences. There is building evidence that acid rains, snows, and fogs, and dry deposition of sulfates are also involved in the deterioration of forests in many parts of the Northern Hemisphere. The details of what is going on are still in dispute, but there would seem to be no sound scientific basis for not immediately moving to abate the injection of sulphur and nitrogen oxides into the atmosphere. The potential long-term impacts of acidification of waters and soils are frightening to contemplate. Among them are dramatic declines in agricultural productivity; destruction of forests with a loss not only of their products but of their flood-control, soil protection, and air-purification functions; and the loss of the nutritional and recreational resources of fresh

waters. A discussion of acid precipitation can be a point of departure for explaining the complexity of forest-soil or aquatic ecosystems. It is also an excellent place to introduce a discussion of the "let's wait and do more research" approach to the solution of environmental problems.

The ecology of nuclear war

The environmental consequences of either the CO_2 buildup or of continuing acid precipitation could be catastrophic. But they would still be minor perturbations compared with the consequences of an all-out nuclear war. Such a war, which in a matter of minutes could kill or fatally injure almost half of humanity, could create ecological conditions that in a few months would exterminate most or all of those who survived the immediate effects (Ehrlich *et al.*, 1983, 1984; Turco *et al.*, 1983; Covey *et al.*, 1984; Ehrlich, 1984*a*).

The section on environment is probably the best place to introduce the topic of nuclear war into the coverage of human ecology. The possible role of population–resource–environment problems in *causing* nuclear war should also be covered when the interactions of various factors are being considered. This topic can be used to introduce students to the kinds of "surprises" that can emerge as any large-scale environmental problem is investigated. With nuclear weapons, the main surprises have been the discovery of the significance of radioactive fallout, electromagnetic pulse, ozone depletion, and finally the entire syndrome of ecological effects that now go under the rubric of "nuclear winter."

The uncovering of the nuclear winter effects can be traced from early discussions of the possibilities of major climatic effects (Stonier, 1964; Ayers, 1965; Ehrlich, 1969; Ehrlich *et al.*, 1977; Ehrlich and Ehrlich, 1981), through the first calculations of the attenuation of sunlight (Crutzen and Birks, 1982), the first computer-modeled scenarios (Turco *et al.*, 1983) and the evaluation of their biological effects (Ehrlich *et al.*, 1983), to the confirmation by the scientific establishment that a nuclear winter was a real possibility (NRC, 1984).

It makes little difference whether the calculations done by Turco *et al.* are based on assumptions that are somewhat too optimistic or somewhat too pessimistic. In either case, the biological effects are so devastating as to make the uncertainties in the physical scenarios relatively trivial. For example, a depression of growing-season temperatures to tens of degrees Celsius below zero is not necessary to bring on catastrophe. Indeed, a drop of average temperature as little as 5°C over most of the northern continental land areas could be enough to destroy virtually all grain agriculture there and bring on an unprecedented global famine.

The coverage of the ecology of nuclear war should not just deal with the nuclear winter effects of darkness and cold. A global smog, levels of ionizing radiation high enough to affect ecosystems seriously, an increase in UV-B (caused by a thinning of the ozone layer by nitrogen oxides generated by thermonuclear fireballs), huge areas swept by wildfires, heavy siltation of rivers and oceans, and the release of toxic chemicals from storage tanks all should at least be mentioned (Ehrlich, 1984*b*). And the point can be made that a full-scale nuclear winter would simply hasten the process of ecosystem destruction that is already under way because of humanity's other actions.

The topic of nuclear winter provides an excellent place to review or introduce a number of basic biological topics in a highly "applied" context. One is the fundamental importance of photosynthesis in powering all significant ecosystems. Those systems can be contrasted with the rare ones based on chemosynthetic organisms (students can be advised to move to the Galapagos trench near a "black smoker" if they wish to be independent of photosynthesis and thus safe from a nuclear winter). Another is the physiological ecology of cold hardening and hibernation. A third is the role of ultraviolet radiation in orientation of insects (in connection with the increased UV-B flux).

Risk analysis

The coverage of nuclear winter is also a good place to introduce briefly the topic of risk analysis. As a first approximation, the risk of an event can be considered as the probability of the event occurring,

multipled by some measure of its severity should it occur. If there is a nuclear war large enough to generate a nuclear winter (the only kind that military analysts think likely), the second factor (the severity) is so gigantic that the risk (probability × severity) remains huge as long as there is even a tiny probability of the event occurring. In the case of a nuclear winter, policy makers need not wait until the probability of occurrence can be closely calculated to take action, because that probability has relatively little effect on the risk. Parallels can be drawn with other potential causes of large-scale destruction of ecosystems such as continued acid precipitation.

INTERACTIONS

Regardless of the time devoted to human ecology in an introductory biology course, a significant fraction of it should be set aside to emphasize the interactions among the key factors. For example, not only would a nuclear war decimate the human population, destroy vast resources, and prove environmentally catastrophic, but human population growth, resource depletion, and environmental degradation all contribute to the tensions that may generate a nuclear war (Choucri and North, 1974, 1975; Ashley, 1980; Choucri, 1984; Ehrlich and Ehrlich, 1985). There are many other examples that can also be used to illustrate the kinds of interactions that must be considered. For example:

1. The age structure, nutritional status, degree of crowding, and purity of water supply of a population all are among the factors that determine its susceptibility to epidemic disease. But an epidemic also could affect all of those factors—by changing the age structure, reducing nutritional status (by killing off farmers, disrupting the transport system, and/or increasing the nutritonal needs of infected individuals) or enhancing nutritional status (by leaving fewer people to divide up limited food supplies later), reducing the purity of the water supply (by direct contamination or by the illness, death, or flight of those whose job it is to maintain water purification facilities), and so on.

2. Energy mobilization systems influence the political structure of a society. A society based largely on dispersed, simple solar energy technologies will be very different from one dependent on large, centralized, complex plants to generate electricity. And if nuclear power is the main source of electricity, its safety requirements demand different kinds of organization than does electricity from fossil fuels.

3. Climate obviously affects agriculture, but the reverse is also true. For example, desertification as a result of overgrazing and clearing of forests for agriculture both increases the albedo of the land surface and modifies local weather (Otterman, 1977; Sagan *et al.*, 1979). Clearing of tropical moist forests can reduce cloud cover because transpiration by the lush vegetation is a major factor in recycling water. This can alter both the albedo and the greenhouse effect (the details are complex), and thereby change local (or even global) climates (Schneider *et al.*, 1978; Thompson, 1979; Schneider and Londer, 1984).

4. Pollution also affects agriculture; various components of smog are toxic to plants and lead to reduced yields. But agriculture is a major source of pollution in forms such as: "pesticide drift," which has led to increased resistance to pesticides in malaria vectors; runoff of fertilizer, leading to eutrophication of lakes and streams; fugitive dust, which may in turn alter climate; and erosion, leading to silt pollution of fresh and coastal waters and declines in fisheries yields.

Many aspects of the population–resource–environment situation may be subject to unfortunate *synergisms*—two or more factors interacting to produce an effect that they cannot produce individually. For instance, malnourished children seldom die simply of starvation, and well-nourished children rarely die of measles. But malnourished children often die of measles and other diseases that they could easily resist if they had adequate diets. Similarly, the total damage done by pollution stresses and by pests in forests and agricultural ecosystems may be greater than

the sum of that done by each separately. Unfortunately, it is very difficult to study the simultaneous impacts of only two factors; detecting all the interactions and synergisms occurring among the multiple insults to which people and environmental systems are subjected is all but impossible.

CURRENT TRENDS CONTINUE

If a large-scale nuclear war can be avoided but current trends continue, what is the likely resolution of the population–resource–environment dilemma? The overriding trend that cannot long continue, of course, is that of population growth. Humanity is already co-opting much more than ten percent of global photosynthesis—even under the most optimistic assumptions limits to population growth are very close. The situation is most starkly revealed in Africa today, where famine due to overpopulation, compounded by political and economic ineptitude, has already condemned millions to premature death. Emphasis should be given to the interaction between population growth and food supplies. If, for example, the African food supply could be doubled in the next 25 years, while nothing was done to limit population growth or to provide massive food transfers from North America (if surpluses were still being generated there), the same *proportion* of people would be starving, but their numbers would have doubled because the population would have doubled.

The situation is temporarily better in places like India, but the same grim considerations apply. It seems highly unlikely that the growth of the Indian population can be halted by birth control measures before it is twice its present size (*e.g.*, Keyfitz, 1971)—about 1.5 *billion* people. It takes little imagination to see that the odds of India reaching that population size are dim indeed. The population situation in India can be put in context by realizing that its annual *increase* of about 14 million is roughly equal to the population of the Netherlands. The more than 2,500 deaths in the chemical tragedy at Bhopal can be compared with that number of births occurring in India in less than an hour, and it was made up by population growth (births minus normal deaths) in less than two hours.

If current trends continue, the most likely course for humanity is an irregular downward spiral toward catastrophe. Six times as many people died in disasters in the 1970s as in the 1960s, as a result of "human vulnerability resulting from poverty and inequality; environmental degradation owing to poor land use; and rapid population growth, especially among the poor" (Wijkman and Timberlake, 1984).

One cannot, of course, foresee the future; but a plausible scenario is not difficult to construct based on trends already evident. Rates of increase in food production in many areas are dropping back toward or below rates of population growth (Brown, 1984*c*). Even in rich countries, the position of the poor is eroding. In the United States "the gap between rich and poor . . . widened in the 1980–84 period: the rich gained ground and the poor lost it" (Cook, 1984). None of this bodes well for a world in which the poor are already in great difficulty, and where terrorism (soon including, in all probability, nuclear terrorism) seems increasingly to be a way for the otherwise powerless to call attention to their plights.

Unless humanity changes its ways dramatically, the frequency and seriousness of both natural and anthropogenic disasters seems bound to increase. At first, they probably will continue to have their greatest impact on the poor nations and poor people within rich nations. Famines will be increasingly featured on the evening news in the rich nations, local wars even more frequent among the poor, and possibly also a resurgence of epidemic disease in ever more crowded, hungry populations. But gradually the disasters will start to overlap in time and space until the entire world slumps into continuous catastrophe and the differences between rich and poor evaporate. Drastic rises in the death rate would end or reverse population growth. As civilization collapses, human survivors will be faced with grubbing out a living on a biologically depauperate, resource-poor

planet. The prospect is not pleasant, but neither is any other "current trends continued" scenario.

SOLUTIONS

Solutions to the dilemma obviously involve changing current trends before they lead to irretrievable disaster. It must be brought home to students that exponential growth in *any* physical quantity—in numbers of people in the human population, bushels of grain produced, or numbers of TV sets, refrigerators, or digital watches produced—cannot long continue on a finite planet. Neither can exponential depletion of fossil fuels, rich soils, or populations and species of non-human organisms. Impacts can be ameliorated, substitutions made, and carrying capacity expanded in various ways, but all of these measures will inevitably involve diminishing returns, eventually leading to a halt in population growth through the operation of the laws of nature. One can only guess at what "eventually" means in this context; my guess is that unless drastic action is taken, "eventually" means before 2010—possibly much, much sooner.

THE NEED FOR REALISM

A realistic approach to the population–resource–environment crisis must first of all be based on understanding that there are both short- and long-term limits to how much Earth's carrying capacity can be expanded—and that a short-term expansion can mean a long-term contraction. It must also distinguish clearly between temporary fluctuations and long-term trends. For instance, energy policy in most nations has not been firmly established, as it should be, on the assumption that petroleum is going to be increasingly scarce (and thus expensive) over the next half-century. The evidence that this is so is overwhelming. Around 1950, petroleum from giant fields in Arabia and Texas cost about ten cents per barrel to discover and produce. By 1971 oil from arctic Alaska cost about $5 per barrel, and in 1983 British North Sea oil cost about $15 per barrel (Cook, 1983). Short of discovering vast new reserves (not impossible, but considered highly improbable by most geologists), the basic upward trend in cost will continue, to the potential detriment of all human enterprises dependent on liquid fuel.

This does not mean that there will not be fluctuations in the price, including substantial short-term drops, as market forces operate, but humanity would be insane to plan for anything but increasing scarcity of this crucial resource. And those plans should include husbanding it and other fossil fuels, both to reduce environmental deterioration and to stretch supplies while suitable substitutes are developed.

The same long-term trend seems inevitable for food, indeed for most commodities. In part, this is because their production costs are increasingly influenced by the price of energy. And in part it is because humanity is exhausting (and paving over) the richest, most easily farmed soils, depleting the highest grade ore deposits, and generally "using up" economies of scale. The most important case of the latter phenomenon may be in fertilizer application in many areas. In Japan, the Netherlands, and the corn belt of the United States, fertilizer use is already so high that further increases will not give significantly greater yields (Brown, 1981).

Unfortunately, there are no substitutes that can be developed for food. But with great care an *ecologically sound* agricultural system could be developed that would temporarily support a large human population—perhaps one somewhat larger than today's—until the population can be reduced to a permanently sustainable size.

Not everything will go up in price, however. Many manufactured items will become cheaper as a result of technological advances as, for example, computers and VTRs have done. And developments in genetic engineering might permit significant advances in agriculture and keep food prices down for a while. But it is a fundamental error to believe that technological solutions can be found that will permit simultaneously a vast further expansion of the human population and a significant rise in the average standard of living. Designing and deploying advanced computer technologies (or space probes) are scientif-

ically, socially, and economically trivial and simple-minded exercises compared with designing and deploying gigantic systems of food production and energy use that do not degrade Earth's carrying capacity. People can live rich and rewarding lives without computers; they cannot live without food and the support of ecosystem services.

THE BASIC SOLUTION

Students should be introduced to the broad outlines of what must be done if humanity is to avoid a catastrophic denouement. The basic solutions to the population–resource–environment dilemma can be summarized very briefly:

1. Stop human population growth as soon as humanly possible.
2. Keep the birth rate slightly below the death rate for a period long enough to reduce the population to a size safely below the long-term carrying capacity (the process should take more than a century—ample time to arrive at suitable estimates of that carrying capacity).
3. Design a "sustainable" society—one that can function without large-scale war, tremendous economic inequity, racism, sexism, religious prejudice, and, especially, without an economic system requiring perpetual growth in physical throughput. The population size of a sustainable society should be well *below* the apparent carrying capacity, to allow a buffer against natural disaster and miscalculation. The society will have to live on its resource "income," not on its resource "capital."

Number 3, of course, amounts to virtually reorganizing civilization. The details of how it should be done are only vaguely grasped at present and are clearly beyond the scope of the human ecology section of a basic biology course. But students should at least be introduced to the notion that "bandaids," minor changes in how society functions, will not suffice to solve our long-range problems. The better students should be encouraged to sample the brilliant writings of Herman Daly (*e.g.*, 1977) on the subject of steady-state economics—to see that reorganizing society really should be possible. All should be encouraged to think creatively about how a sustainable world might be designed, and how we could get from here to there.

ETHICAL ISSUES

The necessary solutions to the population–resource–environment predicament involve various kinds of ethical dilemmas. Controlling the size of the population, to some people, is an evil in itself. The techniques used to persuade (or force) people to have smaller families raise ethical questions. So do various methods of family limitation. So do the differential impact of population and pollution control programs on peoples of different ethnic groups and economic classes. But, of course, *lack* of such control programs also produces differential (and eventually catastrophic) consequences. Needless to say, when the ethics of population and pollution control are discussed, students should be referred to Garrett Hardin's classic (1968) article "The tragedy of the commons."

Choices among energy technologies also involve difficult questions of who pays the costs and who reaps the benefits (Holdren, 1976). And careful planning would be required to make a transition to a steady-state economic system without causing differentially severe hardships for those people and nations at the bottom of the economic ladder.

Ethical problems involve more than just trying to deal justly with various individuals, constituencies, and nations at present. One must also consider questions of intergenerational equity. How fast, for example, can this generation ethically consume humanity's stock of non-renewable resources? Is it moral to commit hundreds of future generations to fail-safe guarding of nuclear wastes?

Perhaps the most difficult class of ethical problems facing those concerned with designing a better future also involves evaluation of the consequences of proposed actions. These problems are most widely recognized and discussed in the context of aid programs, especially emergency famine relief. What is the morality, for example, of giving such relief if there is no significant accompanying attempt to start on the road to population control or to provide

assistance for developing a sustainable agricultural system? Without such programs, the chances seem high that people will be saved today to continue a marginal subsistence, reproduce, and eventually generate an even worse famine in which even more people die and in which the carrying capacity of the area is reduced even further.

UNINFORMED OPTIMISM

A major barrier keeping humanity from moving toward solving its dilemma is that many "cornucopians"—especially economists (*e.g.*, Barnett and Morse, 1963; Norhaus and Tobin, 1970; Thurow, 1976; Anders *et al.*, 1978) do not understand either the dilemma or the general form of the required solutions. Some believe that physical and biological limits to growth can be circumvented by having only the service sector of the economy grow. Others promote crackpot ideas such as that because some resources can be finely subdivided, they are infinite (Simon, 1981) or that "copper can be made from other metals" (Simon, 1980). Such notions must be carefully analysed in class so that students recognize them for what they are. Students quickly grasp that there is no such thing as a service sector of the economy that does not involve expenditure of energy and materials (including those needed to maintain the "servants"), and that there are obvious limits to how much the ratio of services to goods can grow before the economic system would automatically favor a shift toward production of goods (Daly, 1977).

The claim that resources are infinite in quantity because they are infinitely divisible is, quite properly, more confusing to students. Two points should be made in relation to this: first, Zeno's paradox should be explained to the students (Daly, 1982). Zeno "proved" that Achilles could never win a race with a tortoise that had a head start—confusing the infinity of points along a line with its finite length. Simon confused what he thought was an infinite subdivisibility of petroleum or copper with an infinity of the amount of those resources. Second, it should be pointed out that Simon's notion that a resource is infinitely divisible is also incorrect—since at some point in the dividing process (at the level of molecule or atom), further division destroys the resource (separate carbon and hydrogen atoms are not petroleum; separate neutrons, protons and electrons are not copper).

A little analysis also will show, to those students who did not learn in grade school that humanity is not going to convert one metal into another in economic quantities, the impracticality of alchemy. For instance, copper could be produced most cheaply by changing ^{62}nickel into ^{63}nickel in a reactor and then allowing the ^{63}nickel to decay slowly (half-life 100 years) into ^{63}copper. Under ridiculously optimistic assumptions, copper so produced would cost roughly $1.8 billion per pound, and each pound would require some 150,000 railroad cars of coal to produce (A. A. Bartlett and J. J. Kraushaar in Grant, 1982). This is a good place to bring home to students the need for a basic background in mathematics, physics, and biology in all those who wish to enter the discussion on how best to handle problems of human ecology.

Shortsightedness is, of course, not only endemic in the high-discount world of most economists, but extends into other disciplines as well. An example that biology students will find instructive is provided by recent optimism over the prospect of a "victory" over trypanosomiasis (nagana) of cattle through the development of a vaccine (Johnstone, 1984). In the long run, the victory could easily prove a Pyrrhic one. The disease, carried by tsetse flies, effectively bars cattle from substantial areas of central Africa. If cattle could be immunized against trypanosomes, the short-term benefits could be more than balanced by the long-term costs. Introduction of cattle into these areas could result in a great expansion of human and bovine populations, leading in turn to overgrazing, destruction of natural ecosystems, and a dramatic decline in the carrying capacity for both people and cattle (Hopcraft, 1970, 1980).

Cattle are already engines of desertification in semi-arid regions of Africa. Unlike

native herbivores, they require daily water. In their treks to water holes, they trample vegetation, and their feeding patterns follow a heirarchic pattern which destroys the most valuable graze and leaves only relatively unpalatable plants. Their droppings, again unlike those of native herbivores, are not designed to facilitate recycling of nutrients (Hopcraft, 1970, 1980). The bottom line is that large herds of cattle easily degrade African semi-arid ecosystems, destroying first the vegetation and then the fertility and waterholding capacity of the soil. They have been a major factor in the southward spread of the Sahara desert into the Sahel and in the degradation of large areas of land elsewhere in Africa.[2]

Among those concerned with "development," examples of uninformed optimism are legion. Dams and irrigation schemes are often seen as "permanent solutions" to food-population imbalances. But, without population control, they virtually always fail to produce the desired results, even in the middle term. The land brought under cultivation by irrigation from the Aswan dam was inadequate even to feed the people added to the Egyptian population during its construction. Moreover, both dams and irrigation schemes are usually temporary. Dams silt up, and do so especially rapidly in overgrazed or deforested watersheds (because the soil-preserving services of the ecosystem have been impaired). Irrigation canals also silt up, and irrigated land often is rendered unusuable by water logging or the accumulation of salts. And plans for introducing superior management to "solve" problems such as overgrazing in the Sahel are often based on grave misapprehensions of the biological dimensions of the problem (*e.g.*, Bremen and de Wit, 1983).

Perhaps the most serious error made by uniformed optimists is the assumption that humanity has infinite resources, skilled personnel, and good will to bring to bear on any given problem. But the capital that goes into an irrigation scheme in India will not be available to provide decent housing in a Mexico City slum; and the groundwater pumped for the crops will not likely be available to cool a power plant or slake a slum dweller's thirst. Money spent in less developed countries to train skilled engineers to help build the irrigation scheme will not be available to train local biologists and social scientists to help pastoral peoples in Africa stay within the carry capacity of the available range. Resources invested in nuclear power plants can not also be used to plant and harvest biomass plantations or to develop secondary recovery techniques for petroleum. Land put under subdivisions will not be available to grow biomass or food. Dollars and rubles wasted on Pershing II and SS-20 missiles will not be used in soil conservation programs in Iowa or Kazakhstan. Indeed, the money now wasted by the superpowers on unusable and extraordinarily dangerous weapons would be sufficient to double the total rate of investment in poor nations. The North-South Report (Brandt, 1980) estimated that the cost of a ten-year program to take care of the health and nutritional needs of the developing countries would be less than six months of military spending.

Some of the better informed optimists do admit that there are ultimate limits to growth, but claim those limits are far enough in the future that humanity can continue on its growthmanic course for the next few decades. The evidence supports

[2] It is apparent that more people could be supported by many African grazing ecosystems if they were based largely on native herbivores rather than cattle. Antelopes, giraffes, and buffalo partition the plant resources of an area, so that the flora (with which the animals have coevolved) is much less likely to be overgrazed. The native herbivores grow faster than domestic cattle, and their droppings are readily recycled. Recent studies (Hopcraft, personal communication) indicate that game ranching in East Africa can yield at least twice as much meat per hectare as cattle ranching, while simultaneously leading to *improvement* of the range. But the end result of controlling trypanosomiasis in the present cultural milieu is likely to be further disaster for both the African fauna and African peoples. Avoiding tragedy would require a substantial transformation of African attitudes (to many African groups, cattle are a form of wealth) and economic systems, as well as the thinking of aid donors. Here is another case where insight based on biological understanding could lead to solutions.

no such a conclusion; but if it did, would it justify continuing current trends? Only if people cared nothing about their children and grandchildren, who would be faced with the horrendous problems of trying to make a transition to a sustainable society in a much more overpopulated, resource-depleted, environmentally degraded world.

CONSERVATISM

Finally, it is important to emphasize to students the need for a conservative approach to the population–resource–environment dilemma. Why not halt population growth as rapidly and humanely as possible and then see if everyone in that population (perhaps 6 billion people) can be given adequate food, housing, clothing, medical care, educational opportunity, freedom, and leisure? Only if that can be successfully accomplished should humanity listen seriously to cornucopian arguments about how easy it will be to take proper care of an even larger population of *Homo sapiens*. After all, if current trends are allowed to continue and the cornucopians are wrong, even in the absence of a large-scale nuclear war the result could easily be the end of civilization and the premature deaths of billions of people. The problem deserves everyone's attention *right now*. To recommend complacency is to play Russian roulette with the future of our species and our planet.

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The Human Population: Size and Dynamics[1]

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SYNOPSIS. Demography, the study of human population dynamics, is a fundamental part of human ecology. The explosive growth of the human population, especially in the last century, is an underlying cause of the human predicament today and will continue to be for the foreseeable future. A treatment of human ecology in an introductory biology course should acquaint students with the basic concepts and terminology of demography, including a brief history of the human population, a description of the present demographic situation, and the prospects for the future, including the phenomenon of population momentum. The discussion should be cast in the context of the human environment and resource base, including consideration of the size and behavior of the human population relative to the carrying capacity of the planet for human life.

INTRODUCTION

The most significant biological event of the present geological era has been the expansion of the human population from a modest and probably fairly stable size of a few million to several billions in only a few thousand years—an extremely short period compared to evolutionary or geological time scales. Even more significant has been that population's explosive growth from one to almost five billion in less than one and a half centuries and its continuing rapid growth.

The biological significance arises not only from the spectacular change in numbers of one animal species, but also from the impacts of that species on the rest of Earth's biota: especially its co-option of a rising share of resources to support itself, often at the expense of other organisms. Those impacts will be the subject of other papers; this one focuses on human population dynamics. Demography, the discipline that deals with human populations, is virtually identical in structure and concepts to biological population dynamics, although some of the terminology differs. If students are to understand human ecology, it is essential that they become familiar with basic demography.

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VITAL STATISTICS

The human population by the end of 1985 will number about 4.9 billion. It is currently increasing at around 1.7 percent per year, a rate that would double the population in 41 years if it continued unchanged. Some 83 million people were added to the global population in 1984. The increase is accomplished by an average birth rate of 28 births per thousand people in the population minus a death rate of 11 per thousand, producing a net increase (births minus deaths) of 17 per thousand or 1.7 percent (Population Reference Bureau, 1984). (Demographers love to confuse students by using rates per thousand for births and deaths and rates per hundred—percent—for growth.)

These are overall global *average* rates, which conceal enormous disparities between populations of different regions and even within nations (U.S. Bureau of the Census, 1983). For example, the 1984 birth rate in Kenya was estimated to be 54 per thousand, whereas the death rate was 13, giving a growth rate of 4.1 percent. At the opposite extreme, West Germany's birth rate was 10, its death rate was 12, and its growth rate was negative: −0.2 percent. The United States had a birth rate of 16, a death rate of 9, and a rate of natural increase of 0.7 percent (Population Reference Bureau, 1984).

Natural increase differs from *growth* in this case because of immigration, which boosts population growth in the U.S. to over 1 percent per year. Migration obviously can

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strongly influence the growth rate of any nation. For instance, a large, poorly known (because largely illegal) component of immigration to the United States is from Mexico, and Mexico's rate of population growth is accordingly reduced (Ehrlich *et al.*, 1979). This complicates the growth equation above so that it reads:

$$\text{Growth} = (\text{births} + \text{immigration}) - (\text{deaths} + \text{emigration})$$

What are the implications of a human population of nearly five billion, which may double in the next half-century? Why is there such disparity in growth rates among nations? What is the significance of high rates of migration? Why is it so hard to stop population growth? These are questions of considerable importance in human ecology; they also, of course, have great significance for the future of civilization. But to gain an understanding of what it all means, it is necessary to have some appreciation of how the present demographic situation has been shaped by the past.

HISTORY

Before the invention of agriculture ten thousand or so years ago, the human population probably numbered no more than five million. It is estimated that about that many people could have been supported on Earth as hunter-gatherers. From the appearance of the first hominids a few million years ago until *Homo sapiens* had spread to occupy nearly all land areas, the population grew very slowly if at all; high birth rates were nearly balanced by almost equally high death rates. Most historical demographers estimate that crude birth rates would have averaged on the order of 30–40 per thousand population and death rates about the same or slightly lower. Average life expectancies in preagricultural populations probably were quite low—ranging between 18 and 28 years. Of course, some human groups undoubtedly expanded when conditions were favorable, while others experienced population declines or perhaps were even wiped out by natural disasters or diseases (Ehrlich *et al.*, 1977).

The invention of agriculture permitted many more people to be supported on a given land area, and, as agriculture spread, population growth began to accelerate. Whether this increase was accomplished by an increase in birth rates, facilitated by a settled life and more appropriate weaning foods, or by slightly reduced mortality rates, or a combination of both is a matter of controversy (Birdsell, 1968; Durand, 1967; Drumond, 1975). But by the time of Christ and the heyday of the Roman Empire, the human population had increased to perhaps 200–300 million (roughly equal to that of the United States today). After the collapse of the ancient Mediterranean civilizations, the world population continued to expand, though still with local ups and downs caused by good times and bad—bumper harvests and peaceful times or wars, famines, and plagues.

The demographic transition

The dawn of the industrial age in Europe and North America brought improvements in both agriculture and living conditions, which led to another acceleration in population growth as death rates drifted downward from near 40 per thousand toward 25 and even lower, and average life expectancies rose toward 50. But changes in these societies associated with industrialization in the nineteenth and early twentieth centuries also led to a new phenomenon: declining birth rates. This change in birth rates in the West lagged a generation or two behind the falling mortality rates, leading to unprecedentedly rapid population growth rates of 1 percent or more for several decades. The demographic change from a regime of high birth and death rates (known collectively as "vital rates") to low ones became known as the "demographic transition." It was long assumed to be a direct result of industrialization (van de Walle and Knodel, 1980).

Both birth and death rates in the industrializing West slowly dropped throughout the twentieth century, with the exception of the post-World War II "baby boom" in the United States and some other countries. By the 1980s, natural increase in most developed countries was 0.8 percent per year or less. A few countries in Europe had

stopped growing, and some, such as West Germany, were very slowly declining.

The post-war population explosion

The falling death rates that followed the industrial revolution were at first confined to northwestern Europe and North America; then as other countries began to modernize, and particularly as public health and sanitation measures and medical practice improved, their death rates also declined. Just before and after World War II, Western medical technology was exported to the so-called "undeveloped" nations of Asia, Latin America, and Africa, which until then had the high death and birth rates characteristic of preindustrial societies. During the 1950s and 1960s, death rates in those regions plummeted. It was not uncommon to see death rates cut in half in 15 years or less—say, from 32 to 16 per thousand. (This however was still considerably higher than the death rates typical of developed countries, which today are around 10 per thousand.)

But there was little or no change in birth rates, which remained around 40 or more per thousand population. Indeed, changes in birth rates often were *upward*, reflecting the improved health and fecundity of women. As a result, population growth rates in poor nations rose to levels of 2, 3, and even as much as 4 percent per year, far overshadowing the earlier growth rates of industrializing Western nations, which had never significantly exceeded 1.5 percent.

With the explosive burst of growth in less developed nations and continued growth in the industrialized ones, the global population has more than doubled since World War II. The worldwide average rate of population growth is estimated to have peaked at about 2.1 percent per year in the late 1960s (U.S. Bureau of the Census, 1983). Then, as death rates continued to fall, although less rapidly than earlier, birth rates also began to decline in some developing countries, the baby boom ended in the United States, and fertility also declined further in other developed nations. Among the poor nations that succeeded in reducing birth rates, the Peoples' Republic of China is the most prominent and important example, although declines have also been recorded in several developing nations in Asia, the Caribbean, and Latin America.

The consequence of these declines in birth rates has been a slackening of the annual global population growth rate to about 1.7 percent by the mid-1980s. This reduction in the *rate* of growth however has not been enough to offset the increase in the *numbers* of people added to the population each year; the 83 million added in 1984 was the highest ever recorded, and by the 1990s, the annual increment is expected to be around 90 million.

DEMOGRAPHICS

There is a good deal more to demography than birth, death, and growth rates, of course; and familiarity with the basics is essential to understanding the population factor in human ecology. Demographers refer to these rates of change as the "crude birth rate" and the "crude death rate" because they reveal nothing about the *structure* or *composition* of the population or how those rates might change in the future. For instance, a population that has a low crude birth rate might have undergone a severe war that decimated its young men. A low birth rate in that case might be temporary, caused by a skewed sex ratio in the reproductive age-groups. Or a community with many retired people such as Tampa, Florida would have a much lower crude birth rate and a higher death rate than the rest of the United States population because of a skewed age distribution.

In such situations, the "general fertility rate" can provide a somewhat more refined picture of reproductive trends; it measures births per thousand women of reproductive age (usually ages 15 to 44) in the population. Still more refinement can be obtained by looking at *age-specific rates* of fertility and mortality. The age-specific fertility rate is the number of births per thousand women of a particular age in a population. An age-specific mortality rate is the number of deaths per thousand people of a particular age.

In order to take account of fluctuations and differences in age compositions and to

make meaningful predictions of future population trends, demographers use the relatively complex concept of *net reproduction rate*, or NRR (Bogue, 1969). Suppose a computer were used to follow a cohort of 1,000 newborn female infants throughout their lives, subjecting them to the age-specific mortality rates observed in the real population for a particular year, and making those that lived through their reproductive ages bear children at the age-specific fertility rates of that same year. The total number of female babies they would bear, expressed as a ratio to the original cohort, is the *net reproduction rate*. Thus, if the original 1,000 females produced an average of two female children each, the NRR would be 2,000/1,000 or 2 (implying a family size of about four children). An NRR of 1 is known as "replacement reproduction"—each female in one generation is just replaced in the next. An NRR of less than 1 means that the next generation is smaller than the first, but it does not necessarily mean that the population is shrinking.

A simpler concept, and one that is more commonly seen in nontechnical demographic literature, is the *total fertility rate*, or TFR. The TFR is much easier for students to visualize, being essentially the number of children the average woman would bear in her lifetime. Technically, it is defined as the number of children a cohort of women would bear in their lifetimes if they bore all their children according to the age-specific fertility rates in effect at a given time. Unlike NRR, however, TFR takes no account of mortality or of differences in mortality rates. Thus replacement reproduction expressed as a total fertility rate is not 2, but slightly more than 2, because not all women survive to the end of their reproductive years. In developed countries such as the United States with very low mortality rates, a replacement TFR is about 2.1 children per woman; in some poor countries with higher prereproductive mortality rates, a replacement TFR might be as high as 2.4 or 2.5.

In the United States today, the TFR is about 1.9, slightly below replacement. Some European countries have TFRs as low as 1.5 or 1.6. By contrast, in the rapidly growing populations in developing countries, TFRs typically are 4 or more (Population Reference Bureau, 1984). The record is currently held by Kenya, where each woman is bearing an average of 8.1 children.

The momentum of population growth

Populations that have been growing rapidly have very different age compositions than do populations that have had low birth and death rates for many decades. Very large proportions of rapidly increasing populations characteristically are in the younger age classes. Thus, in most developing nations, between 40 and 50 percent of the population are under 15 years old, while only a tiny fraction are over age 65. In slowly growing or stationary populations, such as are found in industrialized nations, by contrast, the proportion under age 15 is less than 25 percent, whereas the fraction of elderly people typically is more than 10 percent.

The preponderance of young people—parents of the next generation—in a growing population explains why population growth cannot be halted overnight by means of birth limitation—a phenomenon known as "the momentum of population growth." Human beings are long-lived animals; their lives normally overlap with those of their children and grandchildren. Even if today's numerous young people just replaced themselves in the next generation, the births of their children and grandchildren would more than compensate for the deaths in today's much smaller older generations. The population therefore would continue to expand for approximately a lifetime—about 60 or 70 years—after replacement reproduction has been reached. Even with successive generations just replacing each other reproductively, the crude birth rate would remain higher than the crude death rate for three generations because parents continue to live alongside their children and grandchildren before reaching ages of high mortality.

Even if a population's reproduction rate has been reduced to *below*-replacement

level, growth may continue for several decades. For instance, natural increase has not halted in the United States, even though the net reproductive rate has been below 1 since 1973. The picture is complicated by immigration, but even if net immigration were halted, at current fertility rates, natural increase would continue until after 2020 because of the higher fertility of the recent past. In that unlikely situation, the United States population would still increase from 236 million in 1984 to over 250 million before beginning a slow decline (Bouvier, 1981). In Europe, the post-war baby boom was brief and comparatively minor in scope; fertility had been quite low since the 1930s; and immigration ceased to be an important factor after 1975. Consequently, a further drop in fertility rates in the 1970s soon resulted in negative population growth in several nations.

The situation in developing nations is entirely different. In most, fertility has declined little if at all. Even under the most favorable circumstances, reducing fertility to replacement level from preindustrial rates requires at least three decades, during which a population may nearly double in size. Because of population momentum, such a population will expand by a large additional fraction before growth stops. A rough rule of thumb is that a population starting with a birth rate of around 40 will expand by 2.5 times from the time the birth rate begins to decline until growth ends. In an extreme case such as Kenya, with a birth rate today of 54, the population might multiply fourfold before growth could be ended—assuming no rise in the death rate.

Four-fifths of the world's population today, almost 4 billion people, are in developing nations. Over a billion are in China, which has reduced its rate of natural increase to about 1.2 percent per year. The average annual growth rate for the 2.7 billion people in the rest of the developing world is 2.4 percent—a rate that has remained quite constant for over twenty years as small reductions in growth in Asian and Latin American countries have been offset by increases in Africa. Because of the momentum built into this huge component of the global population, the entire population is destined to continue growing for a century or so (if there is no appreciable rise in mortality rates).

Population projections

The curve of human population growth, past and projected for the future, is familiar to many biologists. That growth has been roughly *exponential,* which presents an opportunity to explain to students the implications of exponential growth. Not only is it characteristic of recent population growth, exponential growth can be seen in many aspects of the human predicament, including patterns of resource exploitation, increases in agricultural production, and environmental problems. Perhaps the most important lesson for students is that a long history of exponential growth is no guarantee of a long future of exponential growth.

If the human population (or some fraction of it, such as a poor country with a high birth rate) continued to increase at the present rate, that population would rather quickly reach incredibly large dimensions. At a constant 2 percent annual rate of increase, for instance, a population will double in size in 35 years. One hundred people increasing at 2 percent annually will produce 51,200 people in just over three centuries. In that time, 5 billion people could increase to over 2,500 billion—assuming, of course, that they could somehow be supported.

For a long time, unlike population biologists, demographers paid little heed to the question of whether human populations could be supported. In considering changes in population trends, their attention was focused mainly on fertility rates, not on mortality rates. Mortality was expected to continue its long-established trend of decline as nations modernized; whether fertility would also decline appeared more problematical. Human population projections generally showed continued growth at prevailing rates, although it was thought that, eventually, a demographic transition would occur in less developed regions as it had in the industrialized countries.

By the 1970s, fertility in some developing countries clearly was declining. This

led to a new assumption: that populations would eventually "stabilize"—that is, growth would stop and the populations would be stationary.[2] As some populations in industrialized nations made the transition to negative growth, demographers (who sometimes seem to feel threatened by the idea of smaller populations) nonetheless projected for those groups a return of fertility to replacement level within a generation or so (Frejka, 1981).

Most current projections indicate that the world population will reach ten billion or more before growth can be halted and will remain at that level into the indefinite future. Alternate projections by the United Nations, the U.S. Census Bureau, the World Bank (1984), and other demographers offer possible "stabilized" world population sizes ranging from 8 to 13 billion, with the likeliest projections falling between 10 and 11 billion. These projections are all based on different assumptions about the timing of a fertility decline in developing nations; none assumes significant changes in mortality rates other than a smooth continuing decline (Demeny, 1984*a*, *b*), even though reversals in that decline have already occurred in a number of poor countries (Gwatkin, 1979).

CARRYING CAPACITY

What are the implications of a possible human population of twice the present size or more? Can such a population be supported on Earth for any length of time? What is the *carrying capacity* of Earth for human life? Although these questions are outside the normal purview of demography, a basic course in biology is an excellent context within which to address them. Population ecologists, for instance, are accustomed to studying populations of organisms in relation to their resources and environments and in competition with other organisms. By viewing the human population in this light, students can gain much insight into the contemporary human predicament.

The concept of "carrying capacity" is a good place to begin. It is defined by biologists simply as *the maximum number of individuals that can be supported in a given environment* (Ehrlich *et al.*, 1977). For *Homo sapiens*, the question becomes more complex because of the capacity of human beings to modify their environment and to use technology to exploit otherwise unavailable resources, thus in effect expanding their carrying capacity.

But this expansion is nonetheless accomplished at the expense of other organisms on Earth, whose living space and resources have been taken over by people and their domesticated companions. To the extent that populations are dependent on consumption of nonrenewable resources, the expansion is temporary. And it is inevitably limited by the size of Earth itself and the productivity of its biosphere. Human beings already are intensively exploiting over one-ninth of the planet's land surface area for growing crops and their own living space, and another quarter is used less intensively for grazing domestic animals. The fifth or so of land surface still under forest is used in varying degrees for numerous products, including timber and foods, and sometimes also for grazing.

Humanity thus has co-opted to some degree well over half of Earth's land surface to support itself, and generally the most productive portions at that. Moreover, human beings take a significant portion of the biological production of aquatic systems as well. Exactly what fraction of the planet's actual or potential biological productivity is being diverted to support humanity is not known exactly, but it seems to be well over 10 percent. The swiftly accelerating worldwide extinction of populations and species of plants, animals, and microorganisms is an obvious symptom of

[2] There is some confusion in the nontechnical demographic literature between the terms "stationary" and "stable." Technically, a *stationary* population is one that is not growing or shrinking; a *stable* population is one in which the proportions of different age-groups are not changing. Thus a stable population may be growing, shrinking, or stationary. However, in popular literature, the term "stabilization" is often used to mean reaching zero population growth—a stationary population.

displacement as well as of direct damage to ecosystems (Ehrlich and Ehrlich, 1981). In this context, the question of how many more human beings could be supported on our small planet becomes acutely relevant to the problem of population growth.

Thus there may be reasons to think that 10 billion human beings would exceed the carrying capacity of Earth. How many people could the planet accommodate indefinitely? For clues to the answer to this question, one might ask, how well are nearly 5 billion human beings on Earth today being supported? Clearly, some people are very well supported indeed, but most of the world's population is considerably less secure. The vast majority of the world's resources, whether mineral or agricultural, are controlled by only a quarter of the world's population—the citizens of the developed nations. The division between rich and poor populations is the prime political and economic fact of life in the late twentieth century.

Symptoms of overpopulation

Even in wealthy industrialized nations, competition is heightening over such essential natural resources as prime farmland, forests, fresh water, and wilderness and recreational areas. Increasingly, these renewable resources are being degraded by overintensive use as well (Brown, 1984; Holdgate *et al.*, 1982). Moreover, depletion of limited accessible supplies of nonrenewable resources such as fossil fuels and metals has led to rising prices, helping to drive worldwide inflation. And serious environmental problems caused by the use of these resources are not confined to the rich countries (Ehrlich, 1985; Ehrlich *et al.*, 1977).

While population pressures on resources and the environment have become visible in rich nations, they have reached tragic proportions in many poor countries. By the simple measure of their capacity to feed their expanding populations, more and more developing nations are failing the test. Worldwide, perhaps three-quarters of a billion people, mostly in developing nations, are significantly undernourished. UNICEF has calculated that some 15 million children die each year of malnutrition and other poverty-related causes (UNICEF, 1982).

Grain shipments to developing nations have risen dramatically since 1970, and agriculture has become a major focus for development assistance. Yet among the poorest nations—many of which have the fastest growing populations—food supplies remain inadequate (World Bank, 1984). Indeed, in tropical Africa, per capita food supplies *declined* by more than 10 percent during the 1970s and have fallen precipitously in the last two years (Sai, 1984).

In many African countries, average living conditions have visibly deteriorated, and famine is spreading in the wake of a ferocious continent-wide drought. Such occurrences, of course, are catastrophic for people already living close to the margin. Many millions of Africans are at risk of starvation this year, and a massive transfer of emergency food supplies is underway. But the land's productive capacity has been undermined by decades of steadily increasing pressure to support ever more people and their domestic animals. This damage to the land, which possibly helped generate the drought and certainly worsened its impact, may take decades to heal, at best (World Bank, 1984).

A decade ago, the idea that widespread hunger in developing countries was a symptom of overpopulation was denounced by spokespeople from the Third World, who maintained that the planet could feed many times the existing population and blamed their problems on poverty, underdevelopment, inequities arising from the colonial era, and exploitation by rich countries. All these problems have played roles in generating the current dilemma, of course, but overpopulation is an underlying factor that intensifies the effects of the others. The connections among population growth, faltering food production, deterioration of lands, environmental degradation, and economic problems of many kinds (Ehrlich *et al.*, 1977; Council on Environmental Quality, 1980) are more widely

recognized today (Sai, 1984). If students still doubt that overpopulation is a component of the problems of poverty, hunger, and underdevelopment, ask them whether the problem would exist—or be so severe—if the population in question were half as large, or if it were not growing.

A recent study by the United Nations Food and Agriculture Organization (FAO) concluded that by 1975 the populations of some developing regions had already exceeded their food-growing capacities under traditional agriculture, and that populations of several additional regions would outstrip their food-production capacities by the year 2000, even if every square inch of arable land were converted to food production with the most advanced agricultural technology available (United Nations Food and Agriculture Organization, 1982).

Developing countries obviously have no choice but to continue trying to increase their food production. Their demographic structures commit most of these nations to at least a doubling, if not a tripling, of their populations before growth could be halted by even the toughest fertility-reducing policies. While considerable scope certainly remains for increasing crop yields in most developing regions, it must be done with careful planning to create a sustainable system. If not, a large increase in food production might turn out to be only temporary, leading to an eventual collapse after supporting a substantial population expansion.

International migration

Besides increasing pressures on resources and agricultural systems, symptoms of overpopulation can be seen in strains on economic and social systems. One obvious such symptom is the rising trend of international migration. Migrations normally are the result of both "pull" and "push" factors—opportunities that attract migrants to new areas, and intolerable conditions at home, respectively. Sometimes migrations are clearly the result of political events, such as the exodus from Southeast Asia in the wake of the Vietnam war or, earlier, the flood of Cubans to Florida when Fidel Castro took power in 1959. But today migration often is simply a response to rising population pressures in poor countries.

Lack of opportunity for work and sustenance in the countryside, as a result of rapid population growth, pushes millions of rural young people toward cities in developing countries every year. But the expected opportunities in the cities often turn out not to be there; unemployment and underemployment rates in poor countries characteristically are extremely high. In Mexico, for instance, the combined rate in recent years has been estimated in the range of 40 to 50 percent, varying with the health of the economy. Some migrants move to adjacent developing countries where jobs may be available. This can cause trouble later when the workers are no longer needed, as happened in 1983 when immigrant workers in Nigeria were forcibly returned to Ghana.

Opportunities for work in rich countries are comparatively abundant, especially for people willing to work at menial jobs for low wages. So millions of migrants from developing nations have moved to the developed nations, sometimes illegally. The United States receives hundreds of thousands of illegal immigrants each year, as well as about a half million legal immigrants from around the world. How many of the undocumented workers remain in the country is not known; it is known that a large fraction are basically international commuters, traveling back and forth for seasonal work. Most come from Mexico and other Latin American countries (Ehrlich *et al.*, 1979).

The demographic power of immigration is such that, if both legal immigration and fertility continued at their current rates, the United States population would continue to expand until about 2050 and would exceed 300 million before growth stopped (Bouvier, 1981). Continued illegal immigration, or an increase in legal immigration, would prolong growth, perhaps indefinitely. At the least, it would swell the peak population by several tens of millions.

Northern Europe has also been a recipient of migrants from poorer countries, mostly from southern Europe, North

Africa, the Middle East, and South Asia. Because few European nations have common borders with developing countries, they have not been subject to illegal immigration to the same extent as the United States. During the 1960s, when European economies were expanding rapidly but the labor pool was not, many of these nations encouraged immigration from their former colonies. Since 1975, when a recession first drastically slowed economic growth in Europe, immigration has been discouraged and, on occasion, even reversed.

But labor pools in many poor countries are expanding even faster than the population as a whole, because, again, of the age composition of the populations. As the labor pools increasingly outstrip the ability of poor countries to create new jobs, many of the more prosperous developing nations and most of the developed nations will likely be increasingly troubled by immigration from poor countries in the future.

Urbanization

While 75 percent or more of the people in most industrialized nations live in cities, the majority in most developing countries still live in rural areas. But this situation is changing. The same circumstances that lead to international migration are driving people off the land in poor countries and into cities in search of jobs. Throughout the developing world, the populations of cities are generally increasing even faster than the nations, often 10 percent or more per year. The result in many poor countries is the mushrooming of shantytowns around the outskirts of major cities, built by squatters who seem to appear overnight. The shantytowns usually lack even the most rudimentary sanitation or other services such as clean drinking water or public transport. Yet, despite the appalling conditions and lack of employment, shantytown inhabitants seem to feel better off in the city than in the countryside (Ehrlich *et al.*, 1977; Council on Environmental Quality, 1980; World Bank, 1984).

Many cities are becoming overwhelmed with the burden of accommodating and caring for the influx of migrants. Mexico City, projected soon to be the largest city in the world with over 30 million citizens by the end of the century, is already struggling with severe pollution and seemingly insoluble organizational problems. Mexico is trying to develop alternative urban centers to attract the migrants.

POPULATION POLICIES

Before the mid-1970s, opposition to the idea that population growth should be controlled was widespread, especially in developing nations. Maintaining that "development is the best contraceptive," anti-family-planning activists claimed that family planning programs were: (1) undemocratic, because family planning was being imposed on poor countries by the rich nations out of racism or to suppress them economically; (2) ineffective, because such programs had long existed in some poor countries with little success; and (3) unnecessary, because development would both accommodate more people and encourage lower birth rates. While each of these arguments contained some truth, the inherent contradictions among them went largely unnoticed.

Recognition that rapid population growth hinders economic development in poor countries has increased appreciably in the last decade. The presumption that the development process in itself can lower birth rates, however, has proven oversimplified. Traditional measures of development such as per capita GNP and urbanization seem to have little or no relation to fertility. Certain kinds of development, however, which some demographers have described as "social development," as opposed to "economic development," seem to foster smaller families while directly improving people's well-being. The key factors are improvements in nutrition, health, and sanitation, leading to increased life expectancy; education (especially for females); and a strong family planning program (Birdsall, 1980; Cutright, 1983).

Few developing countries now lack a family planning program or a population policy, although the policies of some are only to better the health and welfare of women and children by "spacing" births. Many nations have set goals of ending pop-

ulation expansion, however, and some have achieved impressive success in slowing their population growth. A handful of relatively advanced developing countries have achieved birth rates roughly on a par with the developed nations, although population momentum assures continued growth for several decades.

The Chinese phenomenon

The People's Repulic of China reduced its birth rate by half between 1965 and 1980, and in 1979 startled the world by initiating a policy to encourage one-child families. While much attention has been given to China's difficulties in establishing the policy and abuses that have attended it, very little has been said about the reasons for moving to such a harsh policy in the first place.

China had long been an outspoken opponent of population limitation, asserting that of all resources "people are the most precious." Meanwhile it established one of the world's strongest family planning programs, providing modern contraceptives, abortion, and sterilization, along with basic health services, to people even in remote villages. The contradiction between rhetoric and domestic policy was more apparent than real; a major emphasis in Chinese policy has always been promotion of maternal and child health. Behind a series of apparently arbitrary rules on marriage ages and birth spacing, the goal seems to have been to minimize the number of births while maximizing the health and well-being of each child.

In the early 1980s, Chinese leaders were dismayed to learn that the population was over a billion, about 10 percent larger than previously thought. Like the leaders of many LDCs, the Chinese government had recognized that economic gains were being consumed in accommodating the expanding population. Unlike others, it also had conducted a careful assessment of the nation's resource base and concluded that no more than 650 or 700 million people could be supported on a sustainable basis at a desirable standard of living. China thus became the only nation in the world with an explicit goal not only of ending population growth as soon as possible but also of *reducing* its population by a large fraction (Zheng *et al.*, 1981).

Fertility in China now is approaching replacement level, but population momentum ensures a peak population of at least 1.2 or 1.3 billion before a decline can be initiated, even if the TFR in China falls far below 2 (Yuan Tien, 1983). And such a sharp reduction in fertility will cause considerable contortions in the population's age distribution, which could create serious social problems later. In particular, the Chinese baby boom cohort of the 1960s will create an enormous increase in elderly age classes when it reaches retirement, perhaps comprising as much as a quarter of the population.

Outside China, unfortunately, there is still much resistance to the concept of resource and environmental constraints to population growth, and no other nation has assessed its resource base as China did. Most industrialized nations, including the United States, still lack overall population policies, although birth control information and services are available to the public in most cases. Some developed countries, such as the Soviet Union and Rumania, are even attempting to encourage higher birth rates. It must be remembered, though, that, despite their relatively slow rates of population growth, the citizens of the industrialized nations are the world's major consumers of resources and generators of global environmental degradation.

Means of birth control

The treatment of human ecology as part of an introductory biology course should include, along with demography, some material on the means available today and under development for the future of birth control. Techniques of contraception are perhaps best introduced with a description of the steroid pill, as the best-known example of hormonal control of reproduction. Other forms of hormonal control are also available, including several that are still somewhat experimental. Mechanical methods, such as condoms, diaphragms,

and IUDs, and chemicals such as foam and jellies are also used. Sterilization for either males or females is an increasingly popular method of birth control in developed countries for individuals who have completed their families.

Both contraception and especially abortion have long been matters of controversy and moral debate, and they still are. The latter problem entails the question "when does life begin?" It should be emphasized that, from a biological standpoint, life is a continuum. Sperm and egg are just as much human life as an adult. Similarly, a moss "plant" (like human gametes, the haplophase) is just as much a moss as the tiny moss sporophyte (like adult human beings, the diplophase).

The policy implications of the abortion debate are both complex and very important—at individual levels and for nations and the world. The rights of an unborn, unwanted child are juxtaposed against those of its mother and her present and future wanted children; the rights of unwanted fetuses against the rights of all future generations.

Those who are distressed that 30 to 40 million children are lost each year worldwide because of abortion conveniently forget that the numbers are little changed by the legality or illegality of abortion. The numbers that change are the mortality rates of mothers. History has shown repeatedly that repression of birth control services normally results in a *higher* abortion rate. The only effective way to reduce abortion rates, once the desire to limit families has developed in a society, is to make dependable contraceptives readily available and sterilization services available for couples who want no more children.

Provision of assistance to developing countries to monitor their demographic changes and to support their family planning activities is a significant part of the foreign aid from the industrialized world; yet it accounts for only a small fraction of the billions of dollars transferred in military assistance and only a little more than 1 percent of the roughly 35 billion dollars per year expended for all foreign aid by developed nations and the OPEC consortium combined.

In view of the social, economic, and environmental problems attending rapid population growth, it would be difficult to think of an expenditure more likely to contribute to world security than supporting international population programs. The curiously outdated views of the Reagan Administration, as set forth in policy statements presented to the Second United Nations Population Conference in Mexico City in 1984, were a step backward in the twenty-year-old movement to curb world population growth.

THE BOTTOM LINE

Increasingly apparent constraints on many kinds of resources and growing symptoms of damage to the environmental underpinnings of the entire human enterprise offer strong indications that the rapidly expanding human population is overshooting its carrying capacity. The treatment of human ecology in a general biology course can emphasize this view of the human predicament without dismissing the social and economic complexities that usually preoccupy political leaders. Physical and biological limits apply to populations of all organisms; and humanity is no exception, despite its ability to modify its environment and exploit resources unavailable to other animals. Human beings also differ from all other organisms in their capacity to exercise conscious control over their reproduction. Recent trends in the global food production situation alone suggest no reasonable alternative to a serious worldwide commitment to population control. The merely moderate efforts most countries are making today to reduce birth rates are not sufficient to prevent production of a population far too large to be supported with a decent quality of life for any length of time.

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Science as a Way of Knowing: Man and Food[1]

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SYNOPSIS. The author congratulates the Education Committee of the American Society of Biologists for undertaking the Science as a Way of Knowing project. The project objective, to improve first-year, college-level biology courses, is excellent, and how to handle food and man in the courses is an important issue needing attention.

The author recognizes that course content should vary among institutions because their programs serve widely divergent clientele. Suggestions are made concerning topics which the author believes generally should be given greater attention.

Hunger and famine were recognized as being critical problems in the world, and students should learn more about them. Science is humankind's great hope, and through it the problems the world faces are solvable. Instructors are encouraged to take a positive approach and demonstrate what science can do.

Hunger and famine are largely the result of misguided national and international policies and not the result of our not knowing how to meet the food needs of all the world's people. The challenge is as much to apply what we know as it is to increase our stock of knowledge. This calls for greater emphasis on problem solving.

Teachers are encouraged to view food in its broadest context and call attention to the variations in the *systems* utilized to produce and distribute it. Attention should be given to environmental impacts, efficiency, risk, and managerial requirements for the various systems.

Global food needs in relation to the World's carrying capacity are discussed and information provided on the causes of hunger and famine. Vital issues in food and hunger are discussed.

INTRODUCTION

The Education Committee of the Association is to be congratulated for sponsoring the Science as a Way of Knowing project (SAAWOK) and for devoting a session on the program to man and food. Early this month (December 1984), I returned from Africa, where I once again became painfully aware of the fact that poverty, misery, hunger, disease, and finally, *despair* are a "way of life" for from one-half to three-quarters of the typical developing countries' inhabitants. In many countries, life in the rural areas, where the major economic activity is generally food production, has become too wretched to endure. Millions of people are abandoning the countryside and heading for the cities—seeking jobs that do not exist.

The population data Dr. Anne Erhlich presented is the "straw that is breaking the camel's back." Without major changes in the policies and actions of developing countries and the world community at large, in many countries the bulk of the rural folk and many of the migrants to the cities are doomed to live with the threat of famine continually hanging over them like a threatening storm cloud. Also of recent concern is the increase in hunger in the United States and other industrialized countries where the worldwide economic recession and revised social policies are taking their toll.

DISCUSSION

Is there any hope for the hungry, famine-threatened masses? Yes; and it is science. In the remarks which follow, I hope to show that, in most cases, science already has provided "the answer." We know how to produce the food needed and protect the environment. We can "feed our people." This leads to the first of a series of suggestions which, in my opinion, could improve first year classes.

Suggestion #1: Be realistic, but positive

I recognize that the world is in a mess *vis-à-vis* man and food, but there *is* hope,

[1] From the Symposium on *Science as a Way of Knowing—Human Ecology* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1984, at Denver, Colorado.

and humanity will be better served if teachers take a realistic, but positive, approach. I suggest teachers stress science as a problem solver; point out the risks and dangers from ecological degradation and from the human population explosion, but give "equal time" to showing how the problems could be solved. Demonstrate the role science can play in solving our critical problems.

Suggestion #2: Emphasize "doing"

Our challenge is more than to "know." If we are to "feed our people," we must find ways to move nations and people to act on what is "known." Therefore, I urge teachers of first year biology courses to stress doing as well as knowing. The final section in *Science as a Way of Knowing II—Human Ecology* (Moore, 1985), which I assume all have read, is excellent. The title is "It's Time to Take a Stand"; I agree 100 percent. Perhaps Phase II of SAAWOK should be "Science as a Way of Knowing *and Doing*."

Suggestion #3: Lead students into an awareness of "who benefits most from science and new technology" and "who needs help?"

It is in the Third World where the relationship between man and food—the topic of this session—can be seen in its most direct and fundamental form. It is there where science could "do the most" for people, but it is, in fact, where the least is being done. We who live in the developed world have traditionally benefited most from new scientific discoveries, and among us, the poor have been the last to benefit. Sophisticated technology developed by science which makes heart by-pass surgery, etc., possible is of little direct consequence to the starving people in Africa. Teachers of first year biology and other science courses should stress that "knowing" is important, but for many in the world, it can be sterile. Of course, this is why we—the world—need more than "to know"; we need problem solvers.

Suggestion #4: Expose students to a problem solving approach

A consequence of stressing a "doing" approach should be that students will become better problem solvers. I urge all teachers to foster a problem solving orientation in the classroom and laboratory. The following questions may be helpful to teachers as they review their courses.

On any issue or in any problem area, have the students learned *what* is being done, by *whom*, and *why*?

Have present and future potentials been ascertained (estimated)?

Have the constraints and limitations to achievement of full potential been identified?

How could the constraints be relieved or the limitations by-passed? What are the alternatives? What are the costs?

Has a pragmatic approach been demonstrated wherein various means/ends schemes are weighed against one another? What are the trade-offs?

The above is very sketchy. The point is, I want to urge teachers to organize their courses and present materials in a form which encourages the development of a problem solving mentality.

Suggestion #5: Recognize that the causes of many problems are not biological, and neither are many of the solutions, but they are still proper concerns for biological scientists

There are many constraints which keep humanity (us) from reaping many of the potential benefits from the sciences, and some are in the socio/political/economic arena. Identifying and removing the constraints, wherever they may be, are proper, honorable concerns for scientists. I am pleased Dr. Paul Ehrlich mentioned values in his keynote address. Hunger, even if its major cause is misguided economic policies, is still a proper concern for biologists.

Misguided national policies in both the developing and developed countries are the major causes for millions of people lacking access to the food they need. Enlightened national and community leadership is necessary if corrective action is to be expected. The future leaders of our and many other nations; namely, the influential citizens, will, with few exceptions, be "exposed" to a first year course in biology. Reaching the future leaders with the right material is of tremendous importance. However, leaders

cannot do the job alone. Of greater importance is reaching the rank and file citizenry. Here, we must look to the future teachers in primary and secondary schools. Reaching them should be given high priority, too.

Suggestion #6: Present a thought-provoking global view of food

Beginning biology classes will vary from campus to campus. Each professor must decide what to include. I suggest the following, at minimum:

Define "food" in its broadest context and show how people meet their needs through a system. Students need to know that food is carbohydrates, proteins, etc., and I think we do very well in this regard. However, there is much more to "food"—it is marketing, storage, processing, production (farming), provision of inputs, risk taking, transportation, financing, technology, values, etc. I suggest that after having the students read, and perhaps having a lecture or two on the evolution of agriculture, a detailed description of three food *systems* in typical situations would be helpful. The following are suggested:

a. A "modern" market economy, commercial agriculture-based system.
b. A heavily subsistence-oriented system.
c. A largely pastoral/nomadic system.

In the discussions of the three systems, consider the environmental impacts, use of technology, efficiency (economic and energy), risk, role of government, and managerial requirements. Show where science "fits." Differentiate between the *need* and the *market* for food. Select a country where one of the three systems prevail, and call students' attention to the percentage of the typical family's real income (or effort) which is expended for food. Also, note where each country stands on the development scale.

Review projections on world needs. Need is largely a function of population, and I agree completely with Dr. Anne Ehrlich that in beginning biology, students must be exposed to population projections and to the variations in them. However, don't beat the topic to death. Explain why projections vary. This presents an excellent opportunity to explore the importance of assumptions. Then, accept a creditable projection, and move on to other issues. I suggest using the projections in the United Nations' *World Population Prospects as Assessed in 1980* (New York, 1981). The projection is for 6.1 billion people in the year 2000, and a leveling off by 2050 at 9–10 billion.

Review the worldwide potential for food production. Students need insights into the absolute potentials, and there are numerous studies on the world's absolute carrying capacity. Here, as on other topics, the conclusions vary greatly. On one extreme, it is postulated that, technologically, enough food could be produced to meet the needs of at least 90 billion people! At the other extreme, one can find authors who argue the world cannot continue to support the 4.8 billion some authorities say is our current population.

The more reasonable projections are probably those based on what would be produced if current-day technology utilized in the more developed countries were applied uniformly on a worldwide basis. Under those conditions, world food production would meet the needs of about 9 billion people, which is the leveled-off population projection many authorities I have read say is expected in about the year 2050.

An analysis of the various projections on the world's carrying capacity will probably lead students to conclude that soil loss, threats of deterioration to the environment, etc., are indeed serious problems, but the absolute physical limitation is not a great worldwide issue now, nor will it likely be in the next few years. I believe it is extremely important for students to be exposed to this viewpoint early in their college careers. To identify the great issues requires a narrower and more specific focus. If they do not learn to narrow their focus early in their careers, they will waste much time and energy in later life.

Suggestion #7: In order to improve students' perceptions of "the problem," analyze the current global situation

A situational analysis can be an excellent teaching tool, and there are several good

sources for analyses of the food situation we face today, and will face in the future. Every biology teacher should have ready access to a copy of *Global 2000* (Barney, 1980), *Global 2000 Revisited* (Kahn and Simon, 1983), and Holden's (1983) summary of the two. When students become aware that there is enough food being produced in the world today to meet the dietary needs of all the people, and hunger and malnourishment are not the result of an inadequate world food supply, they will have taken an important step in sharpening their analytical skills. The facts may surprise some college freshmen, but the sooner they get the idea that they must avoid reaching conclusions too quickly, the better. Students should be encouraged to broaden their vistas, and they need to be encouraged to be relevant.

Looking to the future, the *Global 2000* authors (they are on the gloomier side) project food production will increase at 2.2 percent per annum. A paper in *Global 2000 Revisited* projects an annual rate of 2.8 percent. The latter projection assumes no *major* breakthroughs in technology, but does assume continued modest successes in plant breeding. Most of the increase comes from more widespread adoption of current technology and use of production increasing inputs. Since the world's population is projected to increase at 2.5 percent, the idea that the supply of food is not a great global issue per se and the need to "focus in" is reinforced. Students should then be ready to discuss *the issues* in food and hunger.

A booklet entitled *World Food Issues*, is excellent, and I commend it to you. The short, well-researched articles cover the more relevant topics. Every biology teacher should have access to a copy, and parts of it should be required reading for students. I draw heavily from it.

From the global view, the fact that the whole world never goes hungry, or starves, should be obvious to students. I have seen no case where hunger is even national in scope, and this includes Ethiopia today. A wag once quipped, "Hunger is a very personal thing." *Individuals* go hungry, suffer, and die from diseases which strike the weakened body.

To gain the greatest insight into the hunger and famine problem, the relevant questions are "*Who* goes hungry?" and "*Why*?" I think these questions should be asked in beginning biology classes. While hunger and famine strike individuals, the probability it will strike varies by where people live, their class, and their place in the family. Let this sink into the awareness of the students.

The bulk of the hungry and malnourished live in what is commonly called Third World countries. We really do not know how many people suffer from mal- or under-nutrition there, but it is probably a billion or more. With the Third World's population literally exploding as Dr. Anne Ehrlich told us this morning, the situation is likely to get much worse in the next few years.

In the introduction to this discussion this morning, I mentioned that many of those who faced the threat of famine in the Third World are rural people. The *rural sectors*, where poor health, hunger, and malnutrition prevail, are generally characterized by agricultural systems in which the typical rural family, utilizing a minimum of purchased inputs and relying on conventional wisdom-based technology, works a small tract of land or herds a few livestock. The family spends many days of labor to produce a total food supply, which will, under the best of conditions, provide only a meager subsistence. The family that produces the food consumes most of it; therefore, the system may be, and generally is, referred to as the "traditional sub-sector" or the "subsistence sub-sector." Money, including that needed to pay doctors and immunize children (which would make them more productive), is hard to come by. There is little opportunity for off-farm employment, even to process or handle the food which is exported to the urban areas. The real cost of feeding the typical family is very, very high.

In areas where people face the most serious food–nutrition–health problems, production is highly dependent upon weather and other acts of God. When drought,

flood, or pestilence strikes, less than subsistence requirements are available, and people suffer. Frequently, the labor requirements for subsistence or major crops are concentrated into a critically short period; therefore, production cannot readily be increased. Thus, we find massive underemployment most of the year, while farmers complain about the shortage of labor constraining production. In many areas, women provide most of the labor, and in some areas, they are the key production decision makers as well. In vast areas, rapid increases in population and ecological degradation are reducing the resource base per family very rapidly; hence, the number of people on the very edge of survival is increasing.

Dual economies have emerged in most developing countries—a "modern economy" and a "traditional economy." Wages and salaries in the modern economy are high (relatively), and people who break into it have real incomes many times greater (sometimes ten to fifteen times) than those in the traditional economy. People in the modern economy have the money to buy food, and it flows to them. Unfortunately, the modern economy is generally urban-based, and the skills required to break into it are *not* those most rural folk have. The number of jobs in the modern economy is very limited; yet, many go unfilled because the number of people with the skills, attitudes, and experience required is even more limited.

The dual economy concept can also be applied to agriculture. Dualistic agricultural economies have emerged in most of the developing countries—a commercial sub-sector and a subsistence sub-sector. The commercial sub-sector is often export-based; however, in some cases, it is providing the food for urban consumers in the home country. Yields per hectare, production per person per year of labor, and return to investment in the commercial sub-sectors are frequently, perhaps generally, satisfactory. Development strategies in many developing countries concentrate effort on export crops and on the commercial sub-sectors.

The *urban sectors* have generally contained a relatively smaller share of the hunger-prone and sick than have the rural sectors, but there are still plenty. Many, and probably most, of the urban poor are recent rural-to-urban migrants; however, the situation is changing. The crux of the urban food-nutrition problem appears to be the availability of more adequate basic services in the urban areas amid a lack of employment opportunities. Rushing to the cities without the skills required to get a job in the modern, progressive, commercializing and/or industrializing economy, the new arrivee is likely to be disappointed. Many live in slums, which in developing countries tend to be new settlement areas (in contrast to developed countries, where the slums are the old decayed areas).

In spite of all the problems the slum-dwelling, recent rural-to-urban migrant family faces, the total family is likely to be better off than it would have been had it remained in the rural area, and in free societies, it is not likely ever to return to the countryside. Education for the children and health services for all members of the family are likely to be much more readily available in the urban areas—even for the poorest of the poor. If the family was landless before migrating to an urban area, *i.e.*, dependent upon labor only, it may find food cheaper to purchase in the city because of developing country policies designed to hold urban food costs down. Returning to the countryside is not a promising option for the urban poor who are hungry.

Five key terms highlight the food–nutrition–health situation of the developing countries and are extremely important in terms of strategies. They are majority, productivity, income, access, and technical and managerial skills.

The *majority* of the people in most developing countries are dependent upon the agricultural sector for a livelihood. In most developing countries, the majority are in the subsistence sub-sectors of the agricultural sector where *productivity* of the human resource is very low. In agriculture, there are those who have access to land, and there are the landless poor. The latter struggle to find jobs where few exist, and often live an almost animal-like existence, largely on

family, village, or some other form of welfare. Real *income* is extremely low, and the numbers of people affected are so great that the average level of living in a nation so affected cannot be satisfactory. Those who have access to land, while generally much better off than those who do not, frequently lack access to production-increasing inputs and supplies and marketing services. Frequently, the *majority* of the farm families lack ready access to production credit, marketing services, or production-increasing purchased inputs. Almost all—the landed and the landless—lack the *skills and knowledge* needed to become more productive. Low productivity is thus the first order cause of rural poverty; this, in turn, is linked directly to malnutrition, famine, and poor health.

The urbanite on the thin edge of survival is equally likely to be in a family in which the productivity of potential income earners is very low. The problem may be unemployment, underemployment, or employment in an occupation where the reward for work is low. Lacking income, people are unable to buy the food or health care they need. Food and health services are produced largely in response to a money incentive, and both flow to where the money is. This applies to areas, as well as individuals and families. The poor, lacking money, simply cannot channel the flow of nourishing food or health services in their direction.

No discussion of famine is complete without recognizing the crucial role of war and refugees. There are millions of refugees. Almost all are poor, and in their current situation, it is hard for them to be productive and earn income. Obviously, anything that will lessen conflict among nations will reduce famine.

The developed countries have options for solving hunger and famine which are not viable for many of the developing countries. They have the wealth and productive capacity to provide for many people without requiring that they be productive. This is not a very promising option for developing countries.

The potential for developed nations, such as the United States, to increase food production is important and will contribute to the world food supply via international trade, but it does little to solve the basic famine problem. The developing countries, where the bulk of the hungry reside, do not have the foreign exchange needed to buy great quantities of food from abroad. Developed countries are reluctant to continue to give food to any country on a permanent basis. Ultimately, the "food problem" must be solved rather close to where the hungry reside, and the solution will require the poor to become more productive, either in terms of producing more food for themselves or through gainful employment.

The potential the developing countries face for feeding themselves, either through production of food or buying it in the marketplace, varies greatly. Some have vastly underutilized physical resources. Some lie along trade routes and could add value to products in international commerce. Unfortunately, some are "basket cases," and the outlook for them is very dim. The differences among the developing countries was highlighted in a paper to a conference held in 1979 and reported in *Human Resources for Primary Health Care in the Middle East* (Fischer, 1979).

I suggest that each biology teacher call attention to the need for all countries to develop a "food for all" strategy. In each government, somebody should be thinking about food and hunger issues, and providing guidance. Teamwork between government and private sector institutions will be required.

Suggestion #8: Highlight some of the vital issues in food

The booklet cited earlier (Drosdoff, 1984) and entitled *World Food Issues* is an excellent source, and the various articles provide insights into the problems and their potential solutions. The articles take a look at topics such as plant breeding, plant protection, irrigation and water resources, mechanization, post harvest losses and care, technology development and transfer, agrarian reform, and food aid. All of the

potential topics cannot be covered, but students could get a feel for the breadth and diversity of what is involved in modern humankind meeting what has been called our most basic need—food.

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On the Trail of Atmospheric Mutagens and Carcinogens: A Combined Chemical/Microbiological Approach[1]

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SYNOPSIS. Major ecological problems of our polluted troposphere include airborne toxic chemicals, acid rain and photochemical smog, all three of which are now recognized as being closely related chemical phenomena. We also recognize that in order to develop cost-effective strategies for their control, which protect public health and the environment, there must be close scientific interactions between chemists and biological scientists. For example, of rapidly emerging importance is the development of risk assessment evaluations for specific aspects of each of these problem areas. In preparing such assessments, chemists must define the "exposure," and biological scientists the "effects."

In this paper, I discuss an example of how such close interactions proved indispensible in our search for atmospheric mutagens and carcinogens. Thus, an integrated chemical/microbiological procedure for the isolation and identification of particulate chemical mutagens in respirable diesel soot and ambient particles is described. Emphasis is placed on our use of the short-term, Ames *Salmonella typhimurium* bacterial mutagenicity test as a rapid, and relatively inexpensive, means of following the biological activities of these environmental mutagens through the chemical steps of their separation, isolation and identification from highly complex environmental samples. Possible mechanisms of formation of these particulate mutagens are discussed. They include the reactions of polycyclic aromatic hydrocarbons present on the surfaces of combustion-generated particles with gaseous co-pollutants such as nitrogen dioxide plus nitric acid, and ozone.

In discussing this research on a societally "relevant" problem, we illustrate the importance of "Science as a Way of Knowing." We further suggest that this integrated approach to scientific problem solving by chemical and biological scientists might serve as an example of a discussion topic on human ecology for undergraduate courses in the natural sciences.

INTRODUCTION

Today, there is worldwide concern over the impacts on our health and environment of three major kinds of atmospheric pollution—photochemical smog, acid deposition and airborne toxic chemicals. Interestingly, only 10 years ago they were treated by scientists, control officials and the media as being virtually *independent* of each other. Indeed, attention had been focussed primarily on photochemical oxidants, including ozone and nitrogen dioxide, because the ecological impacts of acid rain and toxic organics were not yet generally appreciated.

We now realize that these phenomena are strongly interrelated chemically. They simply reflect different manifestations of the transport, physical and chemical transformations, and sinks of the wide range of airborne pollutants we release into our troposphere (Finlayson-Pitts and Pitts, 1984, 1985). In fact, these research areas are at the core of the rapidly emerging, integrated discipline of Atmospheric Chemistry.

Clearly, chemists and biological scientists share a common goal—and a common responsibility—to better understand, and to teach our students at all levels, freshmen through graduate school, the facts about such threats to our ecosystem. Furthermore, we should also make clear to our students that we scientists must assist public officials in developing reliable, cost-effective control strategies that protect our health and environment.

As an example, some of us are presently involved in the task of developing *risk assessment* evaluations of the health and environmental impacts of a series of airborne toxic chemicals, including the human carcinogen benzene and the widely used chemical EDB (ethylene dibromide). Such risk assessments are important because they

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provide crucial scientific input to those public officials responsible for making the difficult *risk management* decisions. Their decisions determine the nature and degree of emission controls deemed necessary to protect our health and welfare, and they can cost each of us, student and faculty member alike, hundreds of dollars annually. Obviously, we want the controls to be effective.

We should further make clear to our students that, in formulating such risk assessments chemists generally provide information on the nature, sources, ambient levels and persistence of the toxic species to which we and our environment are exposed. On the other hand, biological scientists must identify and evaluate the nature and degree of their health and associated ecological impacts. In short, atmospheric scientists must characterize the "exposure," and biological scientists must determine the "effects."

Given such profound scientific and societal needs, it should be clear to our students that to solve these ecological problems there must be a productive, symbiotic relationship between our disciplines—one that involves our University teaching and research at all levels.

The great chemist, and Nobel Laureate, Emil Fischer stressed just such a relationship over 75 years ago. Thus, in his 1907 Faraday Lecture to the Chemical Society, he stated:

> The separation of chemistry from biology was necessary while experimental methods and theories were being developed. Now that our science is provided with a powerful armory of analytical and synthetic weapons, chemistry can once again renew the alliance with biology, not only to the advantage of biology but also for the 'glory' of chemistry.

Through the intervening three quarters of a century since his lecture, there no doubt have been some chemists and biologists who might have questioned the strength of this "alliance." However, from my perspective, based on two decades of interactions with biological scientists in research, teaching and government service directed toward understanding and solving problems related to the polluted air environment, our "alliance" is not only alive and well, it is thriving.

To illustrate this point, I shall discuss a research program in a "relevant" area we initiated ten years ago at our UC Statewide Air Pollution Research Center (SAPRC) and Department of Chemistry. It has been directed toward the isolation, identification and quantification of the sources and sinks of particulate atmospheric mutagens and carcinogens. The key factor in our progress to date has been our development of *integrated chemical/microbiological* procedures involving large scale use of the Ames *Salmonella typhimurium* assay (Ames *et al.*, 1973; Ames *et al.*, 1975; McCann *et al.*, 1975) as an *analytical detector* for those air pollutants which are bacterial mutagens.

As a chemist, I shall describe how we establish the chemical nature and ambient levels of those airborne particulate mutagens to which the general public is exposed. The task of establishing whether or not these bacterial mutagens are also animal carcinogens—as well as the more difficult challenge of whether or not they constitute a significant risk to public health at the levels we encounter them in ambient air—is left to health effects researchers (see the Proceedings of the Symposium on Biological Tests in the Evaluation of Mutagenicity and Carcinogenicity of Air Pollutants with Special Reference to Motor Exhausts and Coal Combustion Products, Environ. Health Perspect., 1983).

To conserve space, I have limited the number of references. Comprehensive critiques and reviews of the original literature include the National Academy of Sciences reports "Particulate Polycyclic Organic Matter" (NAS, 1972) and "Polycyclic Aromatic Hydrocarbons: Evaluation of Sources and Effects" (NAS, 1983), *Handbook of Polycyclic Aromatic Hydrocarbons* (Bjørseth, 1983) and, more specifically directed to this paper, "Formation and Fate of Gaseous and Particulate Mutagens and Carcinogens in Real and Simulated Atmospheres" (Pitts, 1983).

HISTORICAL

While we may think of air pollution as a relatively recent problem in human ecol-

ogy, deep concern about urban smog was expressed at least as early as the 12th century. In describing the air of Cairo, Egypt at that time, the great philosopher Moses Ben Maimonides stated:

> Comparing the air of cities to the air of deserts . . . is like comparing waters that are befouled and turbid to waters that are fine and pure. In the city, because of the height of its buildings, the narrowness of its streets, and all that pours forth from its inhabitants . . . the air becomes stagnant, turbid, thick, misty, and foggy . . . . If there is no choice in this matter, for we have grown up in the cities and have become accustomed to them, you should . . . endeavor at least to dwell at the outskirts of the city . . . .
>
> . . . [Wherever] the air is altered ever so slightly . . . [you will find men] . . . develop dullness of understanding, failure of intelligence and defects of memory . . . .
>
> Maimonides (12th Century)

Five centuries later in his classic treatise *Fumifugium or the Inconveniencie of the Aer and Smoak of London Dissipated*, John Evelyn described the air quality in 1661 as:

> It is this which scatters and strews about those black and smutty **Atomes** upon all things where it comes, insinuating itself into our very secret **Cabinets**, and most precious **Repositories**: Finally, it is this which diffuses and spreads a Yellowness upon our choycest Pictures and Hangings: which does this mischief at home, is **Avernus** to **Fowl**, and kills our **Bees** and **Flowers** abroad, suffering nothing in our Gardens to bud, display themselves, or ripen;

Evelyn was also concerned about possible health effects of London's 17th Century smog and he noted:

> But, without the use of Calculations it is evident to every one who looks on the yearly Bill of Mortality, that near half the children that are born and bred in **London** die under two years of age*. Some have attributed this amazing destruction to Luxury and the abuse of Spirituous Liquors: These, no doubt, are powerful assistants; but the constant and unremitting Poison is communicated by the foul Air, which, as the Town still grows larger, has made regular and steady advances in its fatal influence."

* A Child born in a Country Village has an even chance of living near 40 years. Much has been said against Mothers who put out their Children to nurse, and where they live in an healthy air, the practice is generally unjustifiable; but the chance for Life in infants, who are confined in the present foul Air of **London**, is so small, that it is highly prudent and commendable to remove them from it as early as possible.

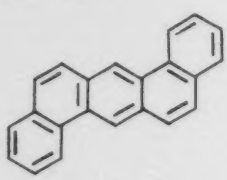
Evelyn's air pollution classic, and the article of Barr, *The Doom of London*, are reprinted in James Lodge's book, *The Smoake of London. Two Prophecies* (1969); it makes interesting and useful reading for students and faculty, and helps place our present problems in perspective.

Carcinogenicity of soot and coal tar extracts

The first observation of the carcinogenic properties of combustion generated soot particles was that of Sir Percival Pott (1775). He proposed that the excess rate of cancer of the scrotum of London's chimney sweeps was due to their infrequent bathing and long periods of heavy exposure to soot. Subsequently, in the latter part of the 19th Century, workers in paraffin refining, shale oil and coal tar industries were found to have high incidences of skin cancer.

In his fascinating article, "Fifty Years of Benzo(a)pyrene," Phillips (1983) traces the history of the subsequent search by biological scientists and chemists for the "coal tar carcinogen" (references to the original literature are found in his article). He notes that in the period 1915–1918, Japanese scientists first showed that painting the ears of rabbits and mice with coal tar extracts produced tumors, some malignant.

Starting in 1922, research by a team of British chemists headed by E. L. Kennaway led to the synthesis of the first pure chemical compounds to show carcinogenic activity, dibenz(a,h)anthracene (DBA), I, and its 3-methyl derivative.



Dibenz(a,h)anthracene

I

Subsequently in 1933, Hewett and Cook isolated from coal tar, and also independently synthesized, the chemically related compound benzo(a)pyrene, (BaP) (see II). They then proved that it was the powerful

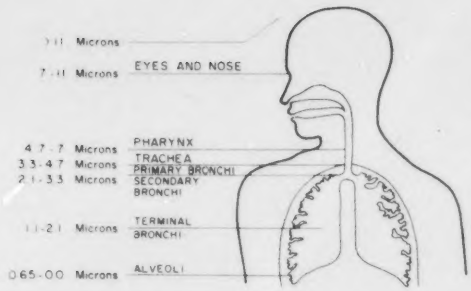
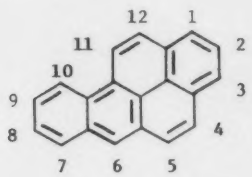


FIG. 1. Penetration areas of different size airborne particles into the human respiratory system.

"coal tar carcinogen." Both DBA and BaP are polycyclic aromatic hydrocarbons (PAH). The currently accepted numbering system for PAH is illustrated in II; the older numbering of PAH was different, a potential source of confusion.

Some 50 years later, BaP



Benzo(a)pyrene

II

is considered an animal, and possibly human, carcinogen." It is well worth examining the IARC monographs on the "Evaluation of the Carcinogenic Risk of Chemicals to Humans; Polynuclear Aromatic Compounds: Parts 1–3," 1983–1984, to establish how this judgment was reached.

Carcinogenicity of extracts of respirable particles in urban air

In the early 1940s, medical researchers in the U.S. showed that organic extracts of particles collected from ambient air were carcinogenic when administered subcutaneously to mice (Leiter *et al.*, 1942). Subsequently, this effect was seen in experimental animals administered extracts from ambient particles collected from Los Angeles smog (Kotin *et al.*, 1954) and other U.S. cities (Hueper *et al.*, 1962). Similar results now have been found for extracts of particulates collected from major urban airsheds throughout the world.

The biological activity of airborne particulates is not surprising because they contain carcinogenic polycyclic aromatic hydrocarbons such as DBA, (I), and BaP, (II), which are *formed* during the combustion of all fossil fuels. Thus BaP was identified in domestic soot in 1949 and in 1952 in ambient particles collected at stations throughout Great Britain.

By 1970, it was clearly established that BaP was present in ambient particles collected throughout the world; sources included diesel exhaust, wood smoke, fly ash from coal-fired power plants, etc. Furthermore, this carcinogen was concentrated in very small, combustion-generated particles with diameters less than ~ 1 μm. This is highly important because these submicron size particles fall in the "respirable" size range and, as seen in Figure 1, can penetrate into the deepest recesses of our lungs and be deposited in our alveoli.

Another interesting fact that emerged in the late 1960s and early 1970s related to the observed carcinogenicity in animals, or rates of transformation in cell cultures, of organic extracts of the fine particles from auto exhaust or ambient air. In several studies, it was found to be significantly *greater* than could be accounted for by the amounts of recognized carcinogens (*e.g.*, BaP, DBA, etc.) determined by chemical analysis to be present in the samples administrated. A key question became: What compounds were responsible for this *excess carcinogenicity*?

We can summarize the situation *circa* 1975 in the following terms:

> Particles generated by the combustion of fossil fuels, and which are present in ambient air, are very small; they fall in the respirable size range, and contain a variety of known carcinogenic compounds (*e.g.*, polycyclic aromatic hydrocarbons such as BaP). Furthermore, their extracts display biological activity well in excess of that predicted for the carcinogens known to be present.

The pronounced societal interest in these fine particles was demonstrated in Section 122a of the 1977 Amendments to the U.S. Clean Air Act which required the Administrator to:

> Determine whether or not emissions of polycyclic organic matter (POM) into the ambient air will cause, or contribute to air pollution which may reasonably be anticipated to endanger public health.

Historically, such a highly specific mandate was somewhat unusual in U.S. air pollution legislation.

In the mid-1970s, our group became deeply interested in tackling the complex problem of isolating, and chemically characterizing, those pollutants which were responsible for the "excess carcinogenicity." However, there were several major stumbling blocks. Such biologically active compounds are present only in trace amounts in the chemically complex environmental mixtures typical of combustion-generated, airborne particulate matter. Furthermore, animal tests for carcinogenic activity were too time consuming and too expensive to be used on a regular basis as major components of "biological activity directed" procedures for the chemical separation, isolation and characterization of suspected carcinogens.

THE AMES TEST: INTEGRATED CHEMICAL/MICROBIOLOGICAL ASSAYS

With the advent in 1973–1975 of the Ames bacterial assay system for detecting chemical mutagens, we felt that we might be able to bypass two of these major problems associated with incorporating animal assays into our procedures for chemical analyses of complex environmental samples. The new Ames' reverse mutation procedure employing histidine-requiring (*his*$^-$) mutants of the bacterium *Salmonella typhimurium* was both rapid (~4 days) and relatively inexpensive. Therefore, we speculated that if we could readily follow the pathways of bacterial mutagens through our chemical procedures, we could isolate and characterize them—and then let the biologists test the pure compounds for carcinogenic activity. Of course we recognized that the observation of mutagenic activity in bacterial assays conducted on environmental samples did not necessarily imply their carcinogenic activity in animals or man.

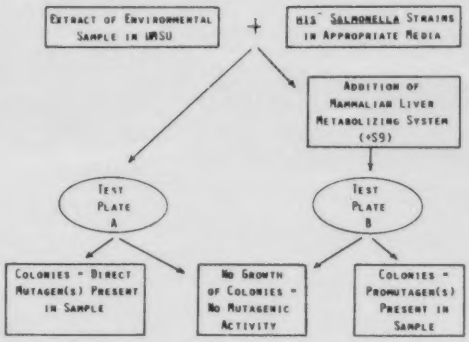

Extract of Environmental Sample in DMSO
+
his⁻ Salmonella Strains in Appropriate Media
Addition of Mammalian Liver Metabolizing System (+S9)
Test Plate A
Test Plate B
Colonies = Direct Mutagen(s) Present in Sample
No Growth of Colonies = No Mutagenic Activity
Colonies = Promutagen(s) Present in Sample

FIG. 2. A chemist's view of the "Ames test."

In short, in 1975 we rephrased our earlier questions concerning carcinogenicity and put them in terms of mutagenicity. Our questions now became:

> Do airborne particles contain chemical mutagens? What are the microbiological clues as to the chemical nature(s) of these particle-bound mutagenic compounds? What are the contributions of various emission sources to the mutagenic burden of particles in ambient air? Can certain polycyclic aromatic hydrocarbons (PAH), which are nonmutagens or promutagens, react with gaseous copollutants in simulated and real atmospheres to form powerful *direct* mutagens in the Ames *Salmonella typhimurium* bacterial mutagenicity assay?

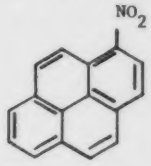
We then began developing procedures for the integrated use of conventional chemical analytical techniques with the Ames *Salmonella typhimurium* assay to determine the mutagenic activities of: (a) extracts of the total samples of airborne particles; (b) samples obtained by chemical and physical fractionation of the original POM extracts; (c) chemical compounds isolated from these fractions and (d) pure "reference" compounds suspected of, or known to be, present in ambient POM and directly-emitted POM (*e.g.*, diesel soot).

A chemist's view of the Ames test

It is beyond the scope of this paper, and my expertise, to discuss in detail the Ames test. Thus I have shown in Figure 2 just the basic elements relevant to our chemical procedures.

Essentially, one first adds serial dilutions of the environmental sample (dissolved in DMSO) to a series of tubes each containing agar and one of the various Ames test strains of bacteria. The resulting solution is then poured onto petri plates filled with minimal salts agar; they are then incubated for ~63 hr at ~37°C. At the end of that time the plates are removed and any colonies present are counted. If a significant increase in colonies above background is observed on Test Plate A (the background is caused by spontaneous *his*$^-$ to *his*$^+$ reversions; the latter can supply their own histidine so colonies can now grow) one can conclude that the environmental sample contained a chemical(s) that is a *direct* mutagen for the particular Ames strain employed.

An example of a directly mutagenic chemical is 1-nitropyrene (1-NO_2-PY) (see III). It is one of a family of nitrated polycyclic aromatic hydrocarbons, NO_2-PAH, which are also called nitroarenes. As we shall see, these nitro-PAH are found in diesel soot, wood smoke and ambient particulates; certain of them are powerful frameshift mutagens on the sensitive and widely used Ames strain TA98.



1-NO_2-Pyrene

III

If no direct activity is observed on Test Plate A, it does not necessarily mean there are *no* bacterial mutagens in the sample. Certain chemicals such as the carcinogenic polycyclic aromatic hydrocarbons BaP and DBA are *promutagens*; they are inactive per se and must be metabolized to more labile intermediates before they can attack the bacterial DNA. Such microsomal activation is achieved by adding to another portion of the test sample a small amount of an enzyme system (+S9, the right hand side of Fig. 2) derived from the liver of rats injected with Arochlor (a polychlorobiphenyl) or other such inducing agents. Now, if a significant number of colonies above background are seen on Test Plate B, then the environmental sample contains promutagens (activatable mutagens).

As suggested earlier, one can obtain a number of valuable chemical clues through use of the enzyme system (S9) and various test strains (*e.g.*, TA98 and TA1535). These are summarized below, and model components given. Note that the numbering system for the NO_2-BaP and the OH-BaP isomers is shown in structure II; note also that ++ means moderate mutagenic activity and + means weak activity.

FRAMESHIFT MUTAGEN (TA98)	BASE-PAIR SUBSTITUTION MUTAGEN (TA1535)
Polycyclic Aromatic Hydrocarbons (BaP) and Nitro-PAH (1-NO_2-BaP)	Alkylating Agents; *e.g.*, β-propiolactone
DIRECT MUTAGEN (−S9)	PROMUTAGEN (+S9)
1-NO_2-BaP	6-NO_2-BaP
ACTIVE MONO-ISOMERS	INACTIVE MONO-ISOMERS
6 and 12 (++):1 and 3 (+) Hydroxy-BaP	2,4,5,7,8,9,10,11-Hydroxy-BaP

Additionally, as illustrated in the discussion on diesel soot (*vide infra*), the possible presence of certain mutagenic mono- and di-NO_2-PAH is indicated by diminished response (relative to TA98) on several nitroreductase deficient *Salmonella* strains (TA98NR) developed by Rosenkranz (Rosenkranz and Mermelstein, 1983).

Our special criteria for the use of the Ames assay in our analytical procedures included:

- It must be sensitive enough to detect trace amounts of mutagens in very chemically complex environmental samples.
- The test must be capable of being car-

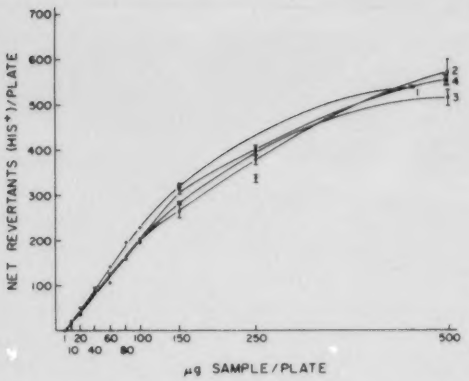


FIG. 3. Direct mutagenic activities (TA98, −S9) of four identical samples of ambient particles collected concurrently using the SAPRC megasampler; 2–3 October 1979, ~10 miles east of downtown Los Angeles, California.

TABLE 1. *Mutagenic activities on Strain TA98, with and without metabolic activation, of organic extracts of four identical samples of ambient particles collected concurrently using SAPRC megasampler.**

Filter number	Total extract mass (mg)	Specific activity (rev/μg)		Mutagen density (rev/m³)	
		−S9	+S9	−S9	+S9
1	22.47	2.4	2.6	73	79
2	23.26	2.0	2.6	63	81
3	24.46	2.0	2.4	66	79
4	23.25	2.1	2.5	66	78
Avg (1–4)	23.26	2.1	2.5	67	79
SD(%)	3.5	8.9	3.4	6.3	1.6

* 2–3 October 1979, El Monte, California; Teflon coated glass fiber filters.

ried out by an "assembly line" procedure so that a large number of plates can be handled at one time (*e.g.*, 600–700 plates per experiment).

- The overall assay must be capable of a high degree of precision (*e.g.*, ±10%) for replicate samples within a given experiment, and good reproducibility between experiments run on different days (*e.g.*, ±20%).

Our initial experiments in 1975–1977 were carried out in a qualitative manner with reproducibilities of the order of ±200–300%. This was satisfactory because our purpose was simply to detect and estimate mutagenicity in a general way in our samples; it was not to use the assay for accurate comparison purposes. Subsequently, with the valuable advice, direction and facilities of Professor William L. Belser, Jr. of our UCR Biology Department, we were able to determine the variables which most significantly affect the reproducibility of the assay. They include, for example, uniformity in the soft-agar layer thickness, temperature uniformity during incubation, incubation interval, etc. (Belser *et al.*, 1981).

An example of the *overall* precision one can obtain if all significant variables in the assay are carefully controlled is shown in Figure 3. This shows the four dose-response curves (strain TA98, −S9) obtained from collecting, extracting with organic solvents, evaporating to dryness and making up in DMSO four identical samples of ambient particles. They were collected simultaneously for 27 hr, 2–3 October 1979, at El Monte, California (just east of downtown Los Angeles) using our SAPRC "megasampler." This was developed by Dr. George J. Doyle and Mr. Dennis R. Fitz of our SAPRC staff for the purpose of simultaneously collecting multiple samples of respirable particulates at flow volumes much greater than those used in regular high volume particulate samplers (Fitz *et al.*, 1983).

After establishing the initial slopes of the four dose response curves (with and without S9), one can calculate: (a) the specific activities of the "identical" aerosol samples (in units of revertants per microgram of solid extracted sample; rev μg^{-1}), and (b) from knowledge of the total volume of ambient air pulled through each filter, the "mutagen densities" (in units of revertants per m^3 of air; rev m^{-3}). Of some relevance to this method of expressing mutagenicity is that an adult human at rest breathes ~11 m^3 of air per 24 hr and about 17 m^3 per 24-hr day at light work.

Our results for the four samples are given in Table 1. Clearly we are, in fact, able to achieve precisions of better than ±10% when our combined sample-collection, chemical-extraction, Ames assay procedure is carefully controlled and carried out.

MUTAGENICITY OF AMBIENT PARTICULATES

The results in Figure 3 and Table 1 show that extracts of ambient particulate matter exhibit strong, frameshift-type mutagenic activity on strain TA98. Furthermore, and most importantly, metabolic activation is *not* required (−S9). Therefore, they must contain direct mutagens.

These 1979 data are entirely consistent with our initial findings in 1975–1977 of the direct activity of ambient particulates collected in southern California air. They are also consistent with those of several other early studies, carried out independent of ours on ambient matter collected in Berkeley, California, two cities in Japan, New York City and Buffalo, New York (for detailed literature references, see Pitts, 1983).

Today, it is generally agreed that:

(1) All urban samples collected throughout the world exhibit direct frameshift activity on strain TA98.

(2) No activity is seen with strain TA1535, which is reverted by base-pair substitution reactions.

(3) Microsomal activation by S9 generally does not significantly increase the activity of the ambient samples tested, except during periods of high traffic activity and at sites heavily impacted by direct sources of combustion-generated POM (*e.g.*, diesel soot, fly ash, wood smoke, etc.).

(4) All mutagenic activity is associated with organic species present in particles less than ~1.1 μm in diameter. Indeed, most chemical mutagens are found in particles less than 0.65 μm in diameter, *i.e.*, in the respirable size range.

It is not surprising that we found extracts of ambient particles were active in the Ames assay when the S9 enzyme system was added. Thus, as noted above, the particles contain PAH such as BaP, which are promutagens. What is most interesting chemically and biologically is that the extracts were also mutagenic *without* metabolic activation. This raises such key questions as: *What are the chemical structures of those compounds responsible for this direct mutagenicity?* and *What are their sources, ambient levels, atmospheric reactions and ultimate environmental fates?*

We shall now briefly address some of these questions to further illustrate the efficacy of combined chemical/microbiological procedures.

DIRECT EMISSIONS OF PARTICULATE MUTAGENS

Shortly after the discovery of the direct activity of respirable ambient particles, researchers at the EPA found that extracts of soot collected from a diesel engine used in a light duty motor vehicle (LDMV) also showed strong mutagenic activities in the absence of S9 activation (Huisingh *et al.*, 1978).

This observation brought quite a response from scientists and control officials because diesel equipped LDMV were then predicted to constitute a significant fraction (~20%) of the new car market by 1985. Indeed, shortly after this discovery, many of the major automobile companies in the world set up facilities and hired microbiologists to conduct Ames tests (and other short-term bioassays) on extracts of exhaust particles from their diesel and spark ignition engines (particles from the latter also contained strong direct mutagens). The approach of combined chemical/microbiological studies had expanded from the worlds of academia and government laboratories into industrial surroundings.

For a discussion of the chemical and biological aspects of this and related problems, see the collected papers presented at the 1982 Karolinska Institute "Symposium on Biological Tests in the Evaluation and Carcinogenicity of Air Pollutants with Special Reference to Motor Exhausts and Coal Combustion Products" (Environ. Health Perspect., 1983), and the Symposium on Diesel Emissions (Lewtas, 1982).

We now know that a substantial share of the direct mutagenic activity of diesel soot is due to the presence of a wide range of mono-nitro-PAH, including 1-nitropyrene (see structure III). This is a strong direct mutagen (specific activity on TA98 ~1000 rev μg^{-1}) and an animal carcinogen. Also present are a series of dinitropyrenes. Some

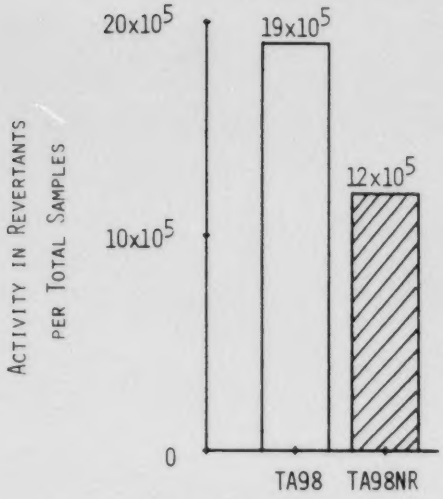


FIG. 4. Direct mutagenic activities (−S9) of the total organic extract of a sample of particulate matter from a light duty diesel engine; strains TA98 and TA98NR.

of the latter are called "super" bacterial mutagens because their specific activities exceed 100,000 rev μg^{-1}; certain of these also have been found recently to be animal carcinogens.

An interesting microbiological clue to the presence of these mono-nitro-PAH in diesel soot is shown in Figure 4. That the extract of the diesel particles contains strong direct mutagens is indicated by the left hand bar; the total activity of the sample on TA98 (−S9) is almost two million revertants. Furthermore, a significant fraction of this activity may be due to the presence of mono-nitro-PAH. Thus, the activity of the diesel sample on the Rosenkranz strain TA98NR (right hand bar) is significantly less than the activity on TA98. TA98NR is an isolate of TA98, deficient in the "classical" bacterial nitroreductase which catalyzes the bioactivation of most mononitro-PAH to their ultimate mutagenic forms. Thus, a lower response to TA98NR relative to TA98 indicates the probable presence of mononitro-PAH in the sample (for an excellent review and critique see Rosenkranz and Mermelstein, 1983).

Professor Rosenkranz and his associates have also developed another strain of TA98, TA98/1,8DNP$_6$, which, while possessing a functioning nitroreductase, is deficient in a second enzyme which activates the potent mutagens 1,8- and 1,6-dinitropyrenes. Consequently, the fact that an extract of diesel soot shows a significant decrease in response on this strain relative to TA98 suggests the presence of dinitropyrenes in the sample (in addition to the mononitro-PAH).

Interestingly, extracts of ambient particulate matter also show diminished responses in strains TA98NR and TA98/1,8-DNP$_6$, indicating the probable presence of both mono- and dinitro-PAH in the respirable particles we breathe. These microbiological clues have been confirmed chemically in several laboratories, including our own. Thus for example, through a series of separations and combined gas chromatographic/mass spectrometric techniques, 1-NO_2-pyrene and several dinitropyrenes have been identified both in diesel exhaust and ambient particles.

Whether or not the presence of these mono- and dinitro-PAH, in diesel soot and ambient particles constitute a health threat to the general population is currently the subject of considerable controversy. Students and faculty alike, in freshman and advanced biology and chemistry courses, might enjoy reading several recent articles on this subject in the journal Mutation Research. Professor Rosenkranz, a microbiologist at Case Western Reserve University takes the "pro" side (*i.e.*, diesel particles may indeed pose health problems for the general population) and Dr. Gibson, a chemist at General Motors, takes the "con" side (Rosenkranz, 1984; Gibson, 1983). This exchange seems relevant to our Symposium theme "Science as a Way of Knowing—Human Ecology" and applicable to several of the points made by Professor John Moore in his perceptive and elegant essay on the subject.

CHEMICAL REACTIONS TO FORM DIRECT MUTAGENS DURING TRANSPORT OF COMBUSTION-GENERATED PARTICLES THROUGH POLLUTED ATMOSPHERES

Combustion-generated particles are not only respirable (<1 μm); some can have

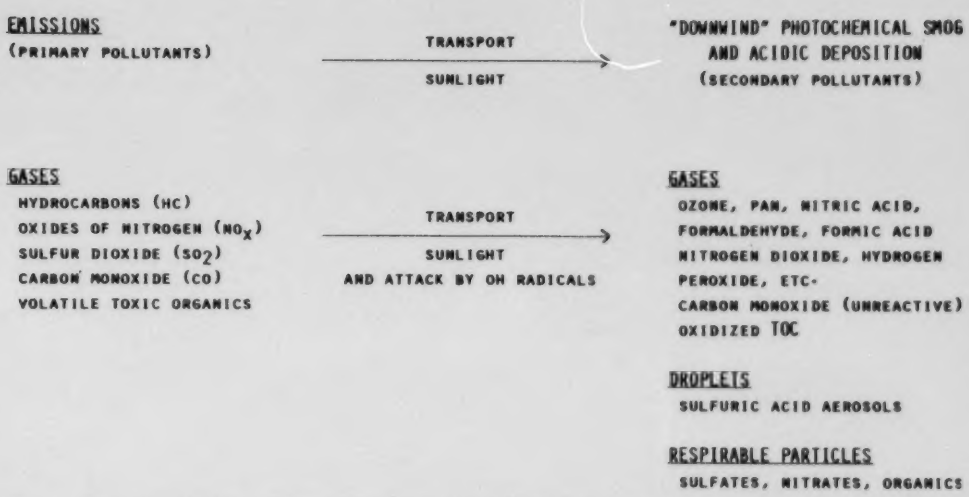


FIG. 5. Examples of daytime chemical transformations in the polluted troposphere showing the conversion of primary pollutants to secondary pollutants.

residence times in the atmosphere (before settling out) of a week or more. In 1976–1977 the thought occurred to us that some of the directly mutagenic species present in ambient aerosols might be produced by atmospheric reactions of PAH present on the surfaces of combustion-generated particles with gaseous co-pollutants found in photochemical smog. As possible reacting species, we knew that the latter contained not only the major, "criteria pollutants" ozone and nitrogen dioxide, but also gaseous nitric acid and other "trace" oxidizing species.

To better illustrate the situation, Figure 5 shows some of the daytime chemical transformations of "primary" pollutants (*i.e.*, directly emitted into the atmosphere) to "secondary" pollutants (*i.e.*, formed in the atmosphere). Note the wide range of products, including ozone, acidic gases and aerosols, and oxidized airborne toxic chemicals. Figure 6 shows schematically the atmospheric "system" (*i.e.*, emissions, transport, transformation, monitoring, of ambient levels, exposure, sample collection, and *in vitro* and *in vivo* assays). Finally, Figure 7 shows the structures of some of the PAH commonly found in combustion generated POM.

We asked the following major questions:

(1) Can a pro-mutagenic and carcinogenic PAH such as benzo(a)pyrene (BaP) deposited on a filter react with ambient levels of gaseous NO_2 + HNO_3 in simulated polluted atmospheres to form directly mutagenic nitro-BaP compounds?

(2) Can pyrene, a nonmutagenic and noncarcinogenic PAH, react with similar synthetic mixtures of NO_2 + HNO_3 to form directly mutagenic nitropyrenes?

The experimental details are beyond the scope of this paper; essentially we simply coated glass fiber filters (of the type used by the EPA to collect ambient particles) with a very thin layer of BaP and passed air containing from 0.25 to 1 ppm of NO_2 (plus ~10 ppb of gaseous HNO_3), through the filter for about 8 hr (Pitts *et al.*, 1978).

That BaP, deposited on a filter, can be nitrated by gaseous mixtures containing ambient levels of NO_2 + HNO_3 is evident from the absorption spectra shown in Figure 8, taken before and after exposure. Three mononitro-isomers are formed; their mutagenic activities are summarized in Figure 9.

In similar exposures, pyrene deposited on a filter was also nitrated, but at a much slower rate than BaP. This reaction order is consistent with established solution phase structure-reactivity relationships for the

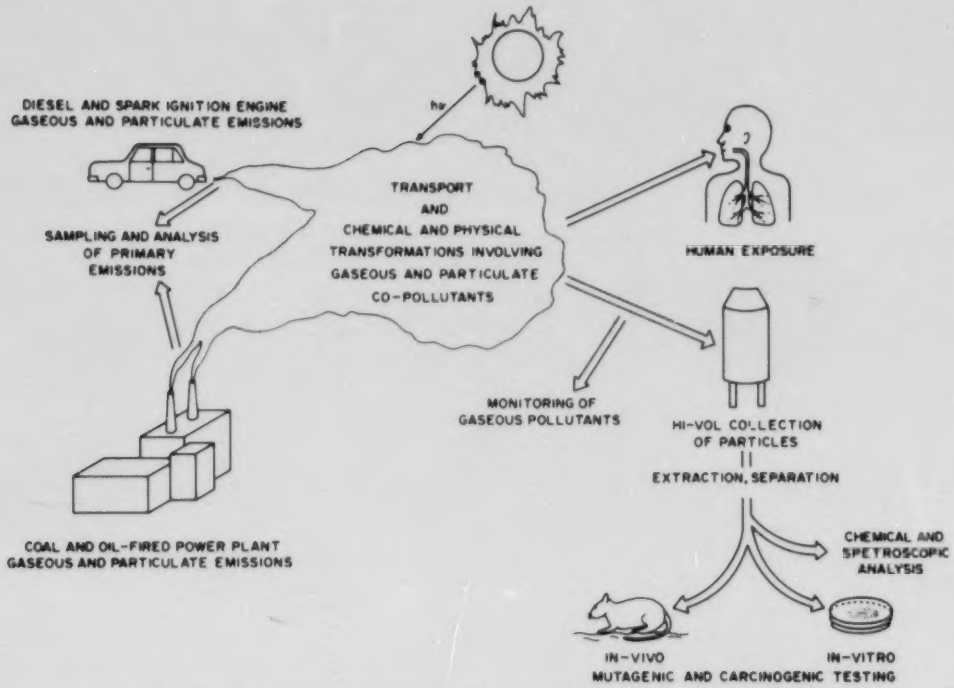


FIG. 6. Primary emissions, transport, transformations and impacts of pollutants.

nitration of BaP versus PY (*i.e.*, BaP ≫ PY). Of particular interest is the fact that the non-mutagen and non-carcinogen, pyrene, was nitrated in a simulated atmosphere, to yield as a major product the powerful direct mutagen and animal carcinogen 1-NO_2-PY (Fig. 10).

Clearly then, we answered some of our questions for simulated atmospheric systems. However, as we pointed out in our original paper (Pitts *et al.*, 1978), whether or not such nitrations by NO_2 + HNO_3 occur for PAH bound on the surfaces of *real* particles in ambient atmospheres is a more complex issue. For example, there may be substrate effects, *e.g.*, BaP deposited on a glass fiber filter may well behave differently than BaP on the surface of an ambient particle. Such questions are currently being explored in several laboratories in Japan, Scandinavia and the U.S.

One other aspect of our results is also relevant to health effect evaluations. Since BaP deposited on a filter reacts with air containing NO_2 + HNO_3, some of the

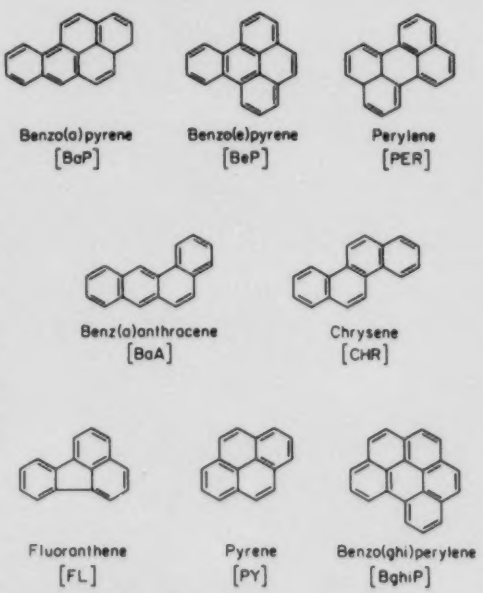


FIG. 7. Some polycyclic aromatic hydrocarbons (PAH) found on the surface of respirable combustion-generated particulate organic matter.

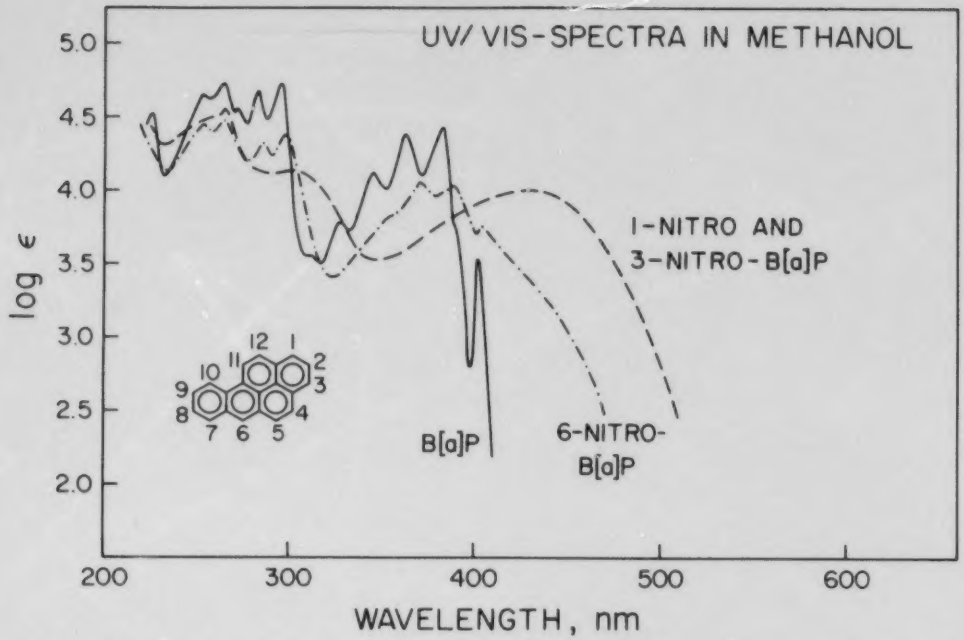
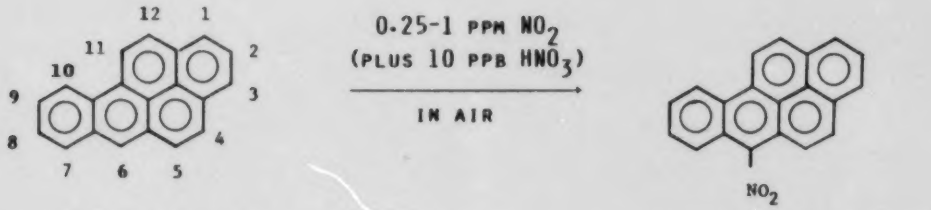


FIG. 8. Ultraviolet absorption spectra of benzo(a)pyrene before, and three mononitro-isomers after, exposure to ambient levels of gaseous NO_2 + HNO_3 in simulated polluted atmospheres.



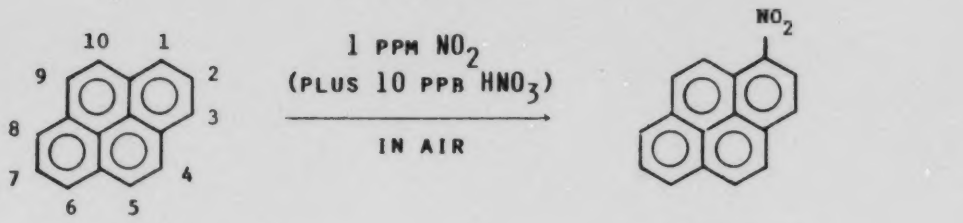
BENZO(A)PYRENE
CARCINOGEN IN ANIMALS
PROMUTAGEN IN AMES TEST

6-NITROBENZO(A)PYRENE
NO DIRECT ACTIVITY IN AMES TEST BUT A STRONG PROMUTAGEN

1 AND 3-NITROBENZO(A)PYRENE
STRONG DIRECT MUTAGENS IN AMES TEST AND STRONG PRO-MUTAGENS

CARCINOGENS?

FIG. 9. Reaction conditions, products and mutagenicities from the exposure of a promutagen and carcinogen, to near ambient levels of NO_2 + HNO_3 in a simulated atmosphere.



PYRENE
NON-CARCINOGEN
NON-MUTAGENIC

1-NITROPYRENE
STRONG, DIRECT AND PROMUTAGEN
IN AMES TEST
ANIMAL CARCINOGEN

FIG. 10. Reaction conditions, major product and its mutagenicity from exposure of a non-mutagen and non-carcinogen, pyrene, to near ambient levels of NO_2 + HNO_3 in a simulated atmosphere.

mutagenic activity (and associated nitro-PAH) found in particles collected from ambient air could actually be produced by gas-particle reactions taking place *on the filter during the actual collection of these samples.* We raised this possibility in our initial paper (Pitts *et al.*, 1978), and the occurrence of such "filter artifacts" subsequently was confirmed. Referring back to Figure 6, such artifacts would mean that the particles inhaled by humans might have different mutagenic (and carcinogenic) activities than those collected on the Hi-Vol sampler, extracted and subjected to chemical, *in vivo* and *in vitro* testing. Studies of the mechanism of formation and importance of such filter artifacts are difficult, but important, and are currently being carried out in several laboratories.

Reactions of polycyclic aromatic hydrocarbons in simulated polluted atmospheres: Ozone

While the presence of certain mono- and dinitroarenes is responsible for part of the direct mutagenicity of ambient particles, there is still a substantial fraction as yet unaccounted for. Other, as yet unidentified, mutagenic species understandably must be present.

It occurred to us that reactions of certain PAH with ambient ozone might also produce direct mutagens. Therefore, we exposed BaP deposited on a filter to synthetic atmospheres containing typical ambient levels of ozone (in much the same way we exposed BaP to NO_2 + HNO_3).

Our initial experiments were qualitative, and showed that BaP reacted readily with ambient levels of O_3 (~0.11 ppm) to form a variety of products, at least one of which was a strong direct mutagen. The next, and far more difficult, problem was how to isolate and characterize this trace mutagenic species. This of course is precisely the type of problem I brought up at the beginning of this paper.

Once again the solution proved to be use of the Ames assay in a combined chemical/microbiological procedure. Figure 11 shows plots of our results for various steps in our analytical procedure, while Figure 12 shows the key reaction and summarizes the mutagenicity results (Pitts *et al.*, 1980).

Part (a) of Figure 11 shows the seventeen fractions obtained from high pressure liquid chromatographic (HPLC) separation of the BaP-O_3 reaction products (note that BaP is given as BP in the figure, and that unreacted BP is fraction 17). The mixture is indeed complex. Without our highly reproducible, "assembly line" Ames assay facility to track down which of those seventeen fractions had significant mutagenic activities, we would have come to an impasse. Because of time and financial constraints, we could not subject ourselves to possibly years of effort in the chemical separation, isolation and proof of structure

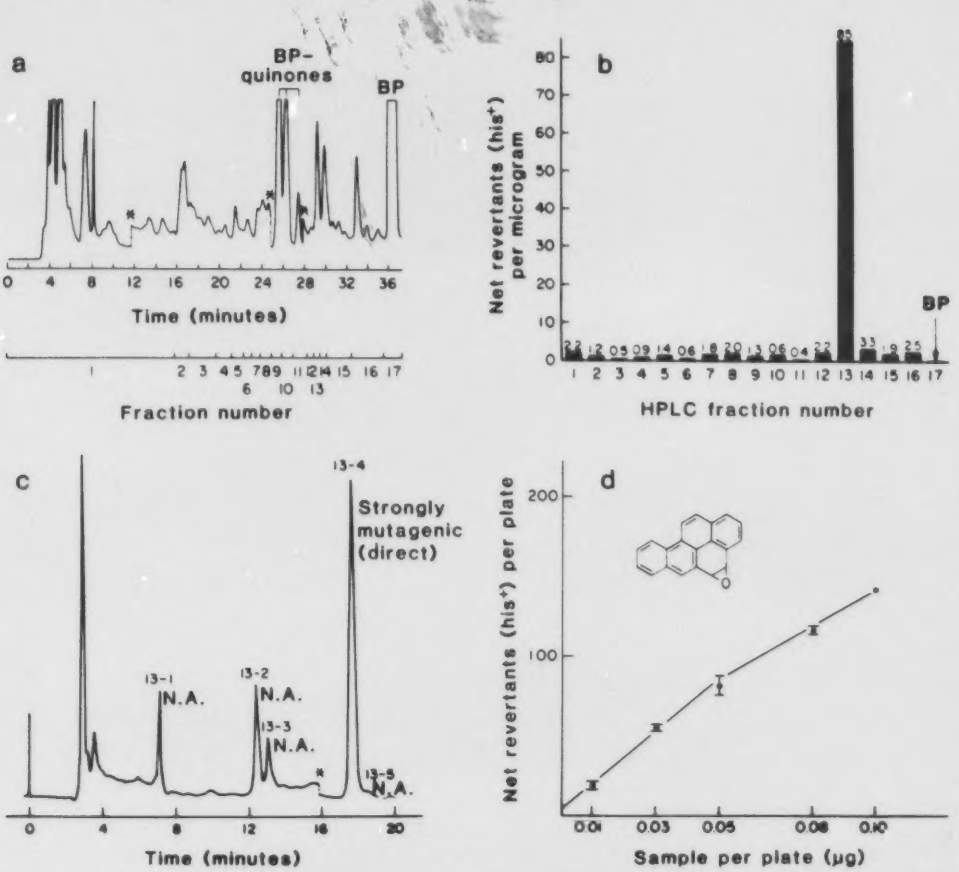


FIG. 11. High pressure liquid chromatograms and Ames test results (TA98, −S9) for an extract of the products of the reaction of BaP (BP) deposited on a filter and exposed to an ambient level of O_3 in a simulated polluted atmosphere.

that could be required to identify the mutagenically "hot" product(s).

Instead, we ran assays on each of the fractions; happily, virtually all of the direct activity towards TA98 was in fraction 13 (Fig. 11b). We then performed another, somewhat different, analytical HPLC separation on fraction 13. It proved to have four components (Fig. 11c). Assays of these showed that the activity resided totally in fraction 13-4; the other three fractions were not active (NA).

Finally, we ran a quantitative assay on fraction 13-4, and from the dose-response curve (Fig. 11d), obtained a specific activity of the isolated product of 1,575 rev μg^{-1} on TA98. Subsequent chemical analysis on fraction 13-4, including fluorimetry, revealed that the product was benzo(a)pyrene-4,5-oxide.

Interestingly, this arene oxide, formed by a reaction in a simulated polluted atmosphere, had been earlier isolated and identified as an *in vivo* metabolite of BaP; it was found by Wislocki and co-workers (1976) to have a direct activity (−S9) of 1,371 rev μg^{-1}. Here again, the worlds of atmospheric chemistry and the biological sciences interface.

CONCLUDING REMARKS

Some general observations on the research we have discussed in this paper include:

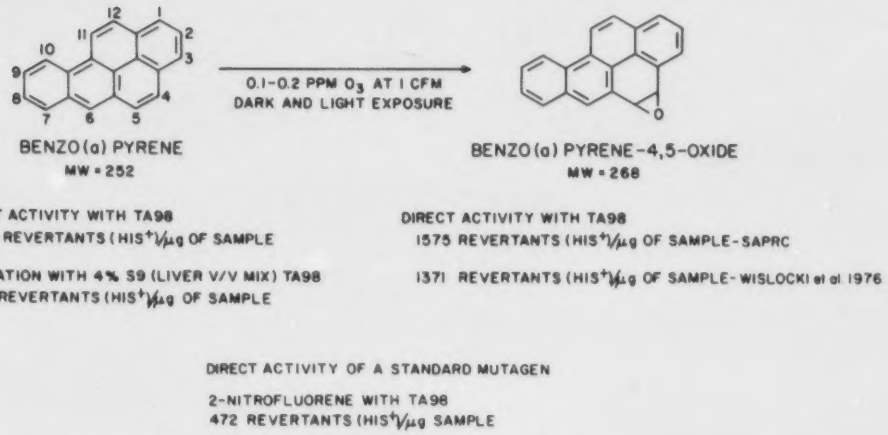

0.1-0.2 PPM O_3 AT 1 CFM
DARK AND LIGHT EXPOSURE
BENZO(a) PYRENE
MW = 252
BENZO(a) PYRENE-4,5-OXIDE
MW = 268
DIRECT ACTIVITY WITH TA98
<1.0 REVERTANTS (HIS+/μg OF SAMPLE
ACTIVATION WITH 4% S9 (LIVER V/V MIX) TA98
386 REVERTANTS (HIS+/μg OF SAMPLE
DIRECT ACTIVITY WITH TA98
1575 REVERTANTS (HIS+/μg OF SAMPLE-SAPRC
1371 REVERTANTS (HIS+/μg OF SAMPLE-WISLOCKI et al 1976
DIRECT ACTIVITY OF A STANDARD MUTAGEN
2-NITROFLUORENE WITH TA98
472 REVERTANTS (HIS+/μg SAMPLE

FIG. 12. Reaction of O_3 in air with BaP deposited on a filter to form benzo(a)pyrene-4,5-oxide, a strong direct mutagen in TA98.

- Polycyclic aromatic hydrocarbons in combustion-generated particulate polycyclic organic matter can be converted in simulated atmospheres to both direct and activatable bacterial mutagens by exposure to air containing ambient levels of (a) $NO_2 + HNO_3$ and (b) ozone.
- Some of these direct and/or promutagens have been identified in diesel soot and in respirable, ambient air particles. They include a series of mono- and dinitro-PAHs, certain of which are animal carcinogens and powerful mutagens in the Ames test.
- Formation of these mutagens may occur in polluted atmospheres and/or during sampling.

Currently, this is an active research field, and I have just touched on several aspects that seem relevant to this Symposium. Areas of particular interest to us now include atmospheric reactions of gaseous PAH emitted in wood-burning and other combustion processes, and the possible role of gaseous dinitrogenpentoxide (N_2O_5) as a powerful *nighttime* nitrating agent of gaseous and particulate PAH.

Finally, in a more general sense, it must be recognized that "what goes up must come down"; these combustion generated PAH, and their nitro- and oxygenated derivatives, ultimately fall out of the troposphere and are deposited in our soil and aquatic systems, including the oceans. Clearly, chemists and biological scientists face even greater challenges ahead when we try to trace the formation, reactions and environmental fates of these mutagens and carcinogens *through* our air/water/soil interfaces.

ACKNOWLEDGMENTS

This paper is based on research carried out in the University of California Statewide Air Pollution Research Center and the Department of Chemistry, and I thank my colleagues, including undergraduate research assistants, for their splendid contributions and support. In particular, I want to thank Drs. Roger Atkinson and Arthur Winer for their leadership roles in these studies and Professor William L. Belser, Jr. of our Biology Department without whose enthusiasm, expertise and generosity in the early days of our work, this program would never have achieved its objectives. I also appreciate many stimulating discussions about this paper with my wife, Professor Barbara J. Finlayson-Pitts, the gracious invitation of Professor John Moore to participate in the Symposium, and the dedicated efforts and professional expertise of Ms. Mae Minnich in the preparation of this manuscript.

Finally, my thanks go to the University of California and to the following agencies that have generously supported research in the areas discussed in this paper: State of California Air Resources Board (Drs. J. Holmes and J. Suder); U.S. Department of Energy (Drs. D. Ballentine, F. Hudson and G. Stapleton) and National Science Foundation (Dr. R. Carrigan).

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Trends in Health—Ecological Consequences for the Human Population[1]

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SYNOPSIS. Rapid health changes in the U.S. and other industrialized nations of the world during the twentieth century are being roughly paralleled in the developing nations, some decades later. These changes include the reduction of communicable diseases, a striking decrease in infant mortality and lower death rates through the age-span, and the emergence and decline of the "modern" epidemics such as coronary heart disease. Increase in life expectancy at birth and at age 65 is one immediate and already measurable impact of these trends. Making several assumptions about the future health of mankind, such as no devastating virus disease epidemics and no further nuclear warfare, one can project three consequences of the health trends described: (1) an almost vertical age-structure of the population, rather than the previous and present pyramidal shape; (2) greater social and individual attention to maintaining health, beyond combatting major diseases; and (3) gradual dissolution of the barriers to association among the peoples of the world.

The Surgeon-General of the United States announced in 1979 that "The health of the American people has never been better." That statement is certainly true by all the usual measures of health.

Until recent years health measurement has concentrated on such questions as: How far have we progressed in curtailing the major diseases and minimizing avoidable deaths? Emphasis has appropriately been on these "negative" aspects of health because the overwhelming health problem of mankind heretofore has been to prevent or overcome disease and to avoid premature death.

Thus, public health people have concerned themselves in the past largely with combatting the epidemic, communicable diseases and infant mortality. The success of such efforts is evident in the world-wide eradication of smallpox and the virtual elimination of cholera, plague, typhoid fever and other formerly epidemic diseases from much of the world. Moreover, a sharp decline in most other communicable diseases has occurred in recent decades (Table 1).

Another measure that is widely accepted throughout the world as a good indicator of health is the infant mortality rate, that is, the number of deaths during the first year of life per 1,000 live births. Table 2 reveals the great strides in reducing that rate, to the point where it is becoming considerably less useful than formerly to indicate health status in such countries as the United States. One must note, however, that the infant mortality rate does delineate the continuing discrepancy in health between favored and less favored populations, for example, between Whites and Blacks, in the United States; and among those living in various countries (Table 3). Thus, although the infant death rate in this country has been declining for some years, the rate among Blacks continues to approximate twice that of Whites. Furthermore, as of 1980, fifteen nations had lower rates than the United States.

Health improvement may also be seen in the falling death rates throughout life, not only in infancy. Examination of mortality trends reveals that quite steadily and at all ages death rates have declined. One way of summarizing that phenomenon is to consider life expectancy, that is, the 50-50 chance that a person of a given age will survive some subsequent birthday. Such a likelihood is based on the age-specific death rates prevailing at the time of the estimate. For example, in the United States during 1980 life expectancy at birth was 74 years, compared with 68 years in 1950 and only 47 years in 1900. The extension of life expectancy from 47 in 1900 to 68 in

[1] From the Symposium on *Science as a Way of Knowing— Human Ecology* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1984, at Denver, Colorado.

TABLE 1. *Selected notifiable disease rates: United States 1950–1980.*

Disease	Number of cases per 100,000 population			
	Year			
	1950	1960	1970	1980
Diphtheria	3.8	0.5	0.2	0.0
Measles	211.0	245.4	23.2	6.0
Poliomyelitis	22.0	1.8	0.0	0.0
Tuberculosis	80.5	30.8	18.2	12.2

Source: National Center for Health Statistics, *Health, United States, 1983,* DHHS Pub. No. (PHS) 84-1232, U.S. Gov't. Printing Office, December 1983, Washington, D.C.

TABLE 3. *Infant mortality rates, United States whites and blacks and selected other countries, 1975 and 1980.*

Country	1975	1980
United States	16.1	12.6
Whites	14.2	11.0
Blacks	26.2	21.4
Sweden	8.6	6.7
Japan	10.0	7.4
Spain	18.9	11.1
Cuba	27.3	19.1

Source: National Center for Health Statistics, *Health, United States, 1983,* DHHS Pub. No. (PHS) 84-1232, U.S. Gov't. Printing Office, December 1983, Washington, D.C.

1950—almost 50 percent in a half century—and similar increases in the other industrialized nations, constituted probably the greatest health advance in the history of mankind.

Improvement is continuing into the second half of the twentieth century and, as noted, extending through the age span. These health advances in recent years are still commonly attributed to success in overcoming the communicable diseases of early life, and the conditions that cause infant deaths. Ascribing health improvement since mid-century to these factors, however, obscures an important development. People in the United States and other so-called advanced nations are now living generally into the seventh, eighth and ninth decades of life. They are no longer cut down by the conditions that accounted for the relatively high mortality rates early in life that prevailed at the beginning of the century. The communicable diseases of the respiratory and gastro-intestinal tracts, which occupied the top rank among the causes of death during the early decades of this century, have been largely overcome. Their places have been taken by diseases of the cardiovascular system and cancer which tend to affect people later in life (Table 4).

As a consequence of this shift, life expectancy has continued to expand. It is now increasing, however, not only as a result of lower death rates during the early years of life but even more as a result of decreased mortality after age 65. The "graying of America" is no longer due primarily to the fact that more people than formerly are reaching the age of 65; it is due to a growing extent to the extension of life beyond that age. Table 5 shows that increase of life expectancy calculated from birth has, in fact, slowed considerably. It is down from

TABLE 2. *Infant mortality, U.S., 1935–1983.*

Year	Total	White	Black
1935	58	52	84[a]
1950	29	27	44
1960	26	23	44
1970	20	18	33
1980	13	11	21
1983	11[b]	9[b]	18[b]

Source: National Center for Health Statistics, *Health, United States, 1983,* DHHS Pub. No. (PHS) 84-1232, U.S. Gov't. Printing Office, December 1983, Washington, D.C.

[a] *All non-white facts of life and death,* DHEW Pub. No. (PHS) 79-1222, U.S. Gov't. Printing Office, November 1978, Washington, D.C.

[b] National Center for Health Statistics, Monthly Vital Statistics Report 32:1–24, 21 September 1984.

TABLE 4. *Death rates for leading causes of death United States 1900 and 1950.*

1900		1950	
Cause of death	Rates per 100,000	Cause of death	Rates per 100,000
All causes (total)	1,719	All causes (total)	964
Pneumonia, influenza	202	Heart diseases	356
Tuberculosis	194	Cancer	140
Diarrheas	143	Stroke	104
Heart diseases	137	Accidents	61

Source: National Office of Vital Statistics, Vital Statistics of the United States, Vol. I, 8:403, 1950.

TABLE 5. *Life expectancy at ages 0 and 65, United States, selected years.*

	At birth	Added	At age 65	Added
1900	47.3		11.9	
1950	68.2		13.9	
		20.9		2.0
1960	69.7		14.3	
1980	73.7		16.4	
		4.0		2.1

Source: National Center for Health Statistics, *Health, United States, 1983*, DHHS Pub. No. (PHS) 84-1232, U.S. Gov't. Printing Office, December 1983, Washington, D.C.

about 4 years per decade during the first half of the century to 2 years per decade more recently. That is not surprising since we seem to be approaching man's natural life-span, perhaps 85–100 years. On the other hand, progress in health during the later years of life was very slow during the first half of the century, about 0.4 years per decade, but the rate of improvement has more than doubled recently. Again, however, life expectancy in the United States has not advanced to the extent attained in several other countries (Table 6).

As more and more people live into their 70s and 80s, largely escaping serious disease for that many years, concepts of health and its measurement are changing. No longer satisfied with avoiding disease and premature death, people are now seeking health in a positive sense, that is, capacity for the full enjoyment of life. Shortly after

TABLE 6. *Life expectancy at birth: Selected countries and selected periods.*

	Years			
	Male		Female	
Country	1972	1979	1972	1979
Japan	70	74	76	79
Sweden	72	73	77	79
Netherlands	71	72	77	79
United States	67	70	75	78
Austria	67	69	74	76

Source: National Center for Health Statistics, *Health, United States, 1975*, DHEW Pub. No. (HRA) 76-1232; and *Health, United States, 1983*, DHHS Pub. No. (PHS) 84-1232, U.S. Gov't. Printing Office, December 1983, Washington, D.C.

TABLE 7. *Physical health spectrum, 1965 residents of Alameda County, California.*

Percent in category	Categories
7	Severe disability
8	Lesser disability
9	Two or more chronic conditions
19	One chronic condition
28	Symptoms only
23	None of above, and low to medium energy
6	High energy level

Source: Belloc, N. B., L. Breslow, and J. R. Hochstim, 1971, Measurement of physical health in a general population survey, Amer. J. Epidemiology 93: 328–336.

World War II the World Health Organization recognized this new situation in defining health as a state of "complete physical, mental and social well-being, not merely the absence of disease or infirmity." That definition opens the possibility of measuring health not in terms of premature mortality or diseases avoided but rather on a continuum extending from some mid-point in a positive as well as a negative direction. One can conceive of health measurement as placing individuals on a multidimensional spectrum, of "physical, mental and social well-being" in the words of the World Health Organization. Every person has a certain degree of health, falling somewhere on the spectrum between severe illness at one end, through

TABLE 8. *Self-assessment of health and limitation of activity, according to selected characteristics, U.S., 1976 and 1981.*

	Self-assessment of health as good or excellent		No limitation of activity	
	1976	1981	1976	1981
Total, age-adjusted	87.9	88.2	86.1	86.3
Family income, age- and inflation-adjusted				
$7,000	77.8	77.5	77.5	77.3
$10–15,000	86.2	87.6	85.0	85.1
$25,000 or more	92.7	93.5	89.6	90.2

Source: Adapted from National Center for Health Statistics, *Health, United States, 1983*, DHHS Pub. No. (PHS) 84-1232, U.S. Gov't. Printing Office, December 1983, Washington, D.C.

various degrees of lesser illness toward the wellness end of the spectrum, and great capacity for the enjoyment of life.

For example, studies in Alameda County, California, over the past 25 years have used this concept. A survey of that county's population disclosed that, based on answers to a health questionnaire, the residents could be categorized quite readily on a health spectrum (Table 7). In the same survey 25 percent of the respondents classified themselves as having excellent health, 56 percent good health, 16 percent fair, and 2 percent said they were in poor health (Kaplan and Camacho, 1983). The National Health Information Survey has revealed nation-wide patterns of health, for example, one based on self-assessment and another on activity limitation; trends over time and among population groups, such as those in various income levels, are illustrated in Table 8.

These and similar efforts to extend the concept and means of measuring health, reflecting the present health situation in many countries, are still quite primitive. Yet they seem to indicate a trend toward concern with the enhancement of health, beyond preservation of life and minimizing disease. A multi-national effort in this direction has been undertaken by the World Health Organization Regional Office for Europe (Abelin *et al.*, 1985).

Thus, health improvement in countries like the United States has created a situation in which the major diseases prevalent at the start of the twentieth century no longer seriously affect the population. People now live typically in good health beyond "three score years and ten," and can even begin to seek health in a positive sense.

While health and ways of seeking it can be characterized in this auspicious fashion, one must also note that industrialization during the twentieth century has brought its own epidemics. In our time as in prior eras, the health of people reflects the conditions of their life. Drought brings famine to people on marginal existence even in 1984. During early industrialization people flocked into the cities where life meant poor sanitation, crowded housing, gross malnutrition and exhausting labor; tuberculosis took a heavy toll, along with acute respiratory and gastro-intestinal diseases. With the advance of industrialized society came plenty of food, especially fatty food, for masses of people; lower physical demands; cigarettes; cheap alcohol. These and other features of current life have brought different kinds of disease into prominence. For example, coronary heart disease, in its most common fatal manifestation—myocardial infarction, was first described as a clinical entity in the United States only in 1912. Before that time it was not even recognized in medical textbooks (Herrick, 1912). During the next 50 years coronary heart disease increased as a cause of death, to account by 1960 for one-third of all deaths in our nation. Lung cancer, a very rare form of malignancy during the early part of the century, also rose dramatically; it is now responsible for about five percent of total deaths in the country and one-fourth of all cancer deaths. These and other chronic diseases affect people typically in the middle and later decades of life, 20–60 years after they adopt a lifestyle that is causative. Thus American women started to smoke cigarettes en masse during the industrial build-up of World War II. Their lung cancer epidemic was predicted to, and did, start in the 1960s. It will continue at least for the balance of this century.

The prototype disease of advanced industrialization is coronary heart disease. Interestingly and contrary to most other epidemics, it first affects the more affluent members of society. It then penetrates the lower social strata as the lifestyle of "modern times" encompasses the whole of society. By the 1970s, however, the epidemic in the United States was clearly receding. It has already declined more than one-fourth from the peak, and especially among more affluent people. In Eastern European countries, on the other hand, the coronary heart disease epidemic, and some other chronic diseases, are just now hitting the populations with full force (Table 9). This latter phenomenon corresponds generally to advances in industrialization and the corresponding lifestyle changes, particularly the greater consumption of fatty foods

TABLE 9. *Mortality rate for coronary heart disease men age 35–64, 1969–1977, several countries.*

Country	1969	1977	% difference
	Decrease		
United States	865	670	−23
Canada	703	624	−11
Norway	583	537	−8
Japan	126	103	−19
	Increase		
Bulgaria	299	424	+42
Poland	187	308	+65
Hungary	442	499	+13
England, Wales	662	672	+1.4

Source: *Report of working group on arteriosclerosis*, DHHS Pub. No. (PHS) 81-2034, U.S. Gov't. Printing Office, 1981, Washington, D.C.

TABLE 10. *Annual deaths from communicable diseases in Africa, Asia and Latin America, 1977–1978.*

Infection	Deaths/year
Diarrheas	5–10,000,000
Respiratory infections	4–5,000,000
Malaria	1,200,000
Schistosomiasis	0.5–1,000,000
Hookworm	50–60,000
Chagas disease	60,000

Source: Adapted from Walsh, J. A. and K. S. Warren, 1979, NEJM 301:967–974.

and cigarettes and lower physical demands at work after World War II. The same factors that altered health in the "Western" countries during the first half of the twentieth century have been determining the health of Eastern Europeans during the second half of the century.

The correspondence between health trends and industrialization does not end there. Upper class Latin Americans, whose lifestyle resembled that of North Americans by the middle of this century, began experiencing coronary heart disease to a significant degree shortly thereafter. A striking illustration of the same trend may now be seen in Papua New Guinea. People in the interior of that nation are leaping from an essentially Stone Age existence that persisted until World War II to a life that is rapidly becoming characterized by motor transport, factories, airplanes and commercial transactions. Coronary heart disease is already appearing among the relatively young men that are leading such enterprises. Meanwhile the current switch in that developing country from chewing betel nut and tobacco to smoking cigarettes is bound to reduce the incidence of mouth cancer but increase that of lung cancer.

Along with the growth of science and technology during this century has come a tendency to assign credit for health advances to the application of technology in medical care. For example, the substantial decline of coronary heart disease mortality in the United States is commonly attributed mainly to the inauguration and spread of coronary care units in hospitals. This view, however, is being challenged and increasingly found wrong by serious students of the issue. Thus, Robert Levy, the Director of the National Heart, Lung, and Blood Institute, said, "It appears to this author that the risk factor and lifestyle changes deserve a good portion of the credit (Levy, 1981). Strong evidence supporting the latter position has recently come from Goldman (Goldman and Cook, 1984).

Studies in Alameda County have shown further that the way people live is highly related to their present and future health, and to subsequent mortality (Berkman and Breslow, 1983). For example, men who follow poor health practices with respect to eating, sleeping, smoking, use of alcohol, and exercise, and who also have weak social networks, die at five times the rate experienced by men with good health practices and strong social networks. In the case of women, the difference is four-fold. Several other investigations come to conclusions in the same direction (Wilson *et al.*, 1981; Brock *et al.*, 1982; Metzner *et al.*, 1983).

The fact that the diseases of industrial civilization are becoming manifest in developing nations just as they are receding in some developed countries should not, of course, obscure the tremendous burden of parasitic and other communicable diseases that still afflict the people of Africa, Asia and Latin America. Tens of millions continue to die each year from these largely preventable causes (Table 10). Deaths from such diseases in childhood and early life

TABLE 11. *Life expectancy at birth in Costa Rica, Latin America and more developed countries 1950–1980.*

	Costa Rica	Latin America	More developed countries
1950	56	46	70
1960	63	56	72
1970	65	60	73
1975	70	62	74
1980	73	—	—

Source: Bixby, L. R., Social and economic policies and their effects on mortality: The Costa Rican case, IUSSP, 28 February–4 March 1983, Paris.

TABLE 12. *Age distribution, population of the United States: 1970–2050.*

Year	All ages	Ages under 25	Ages 25–44	Ages 45–64	Ages 65 and over
1970	100%	46%	24%	21%	10%
2000	100	34	30	23	13
2050	100	29	25	24	22

Source: United States population outlook, Statistical Bulletin, Metropolitan Insurance Companies 65: 16–19, January–March 1984.

are mainly responsible for the general failure of nations in those parts of the world to achieve the life expectancy enjoyed in the industrialized countries. What may happen in a relatively few years, however, may be illustrated by the case of Costa Rica (Table 11). Resembling the other Latin American countries more closely than the developed countries in the 1950s, Costa Rica's life expectancy by 1980 was fast approximating that of the more developed countries, and far ahead of other nearby countries in life expectancy. Finally, it should be noted that the birth rate tends to decline as life becomes urbanized, and sex roles shift, based on industrialization.

In summary of these trends in health, it appears that:

1. The communicable diseases and other conditions that cause deaths especially during early years of life have been largely overcome in the industrialized nations of the world.
2. The health problems that affect people during industrialization, typified by coronary heart disease, are still spreading but also clearly diminishing in at least some developed countries.
3. Developing nations generally repeat this pattern; the longevity of their people tends to approach whatever the natural life-span of man may be.
4. The birth rate declines as urbanization and industrialization advance, and women enter the out-of-home labor force.

These are the main trends in health discernible toward the end of the twentieth century. Estimating the ecological consequences requires several assumptions. One is that no overwhelming epidemics of communicable disease occur. It is still possible that some variant of the influenza virus or something like AIDS could sweep mankind. A second condition is that the birth rate be brought, and kept, under control; man's capacity for accomplishing that task is being well demonstrated in China. Third, and regarded by many of us as the greatest present hazard, the future of mankind depends on avoidance of any further nuclear warfare. Moreover, the ecological consequences of present trends in health—as well as the trend in health itself—depend upon our ability to minimize the effects of man-made toxic materials. The lessons of the cigarette and of asbestos must be mastered. These four assumptions pertain to life as we approach the twenty-first century. In shorter term, of course, it is necessary to take into account many other health and social issues. Of high priority among these is the mass unemployment that is bedeviling so many industrialized countries today, and threatening the developing nations too, as a result of failure to adjust capital-intensive industry to the current needs of people.

Presuming that man will find a way to handle these conditions satisfactorily, one can turn to consider the ecological consequences of present trends in health. I would suggest anticipating three.

First, the size and age-structure of the human population will stabilize at somewhere between five and ten billion with an almost vertical shape to the age-distribution, contrary to the rather sharp pyramidal form of most present populations of the world. One projection based on Bureau of the Census Current Population Reports

indicates the extent to which that may occur in the United States as early as 2050 (Table 12). Until now many, many children have been born only to die at an early age, with moderate numbers reaching middle age, and very few attaining whatever man's lifespan may be—perhaps 85–100. In the future we can expect that families will have typically one–three children, and most of these will live out their biologically achievable years. Thus there will be nearly the same numbers of people at ages 1, 10, 40 and 80. The total number of human beings on the earth will be relatively fixed, rather than rapidly expanding as at present. Grandparents and grandchildren will be of approximately equal numbers.

Secondly, with more years of life expected for enjoyment, greater social and personal attention will be given to maintaining health. The American comedian's remark, "If I'd known I was going to live so long, I'd have taken better care of myself," will no longer be a joke but rephrased into a guide for action. Communal responsibility for health, which has characterized man's existence to varying degrees since his origin, will reach a high point. Society will systematically cultivate conditions for life that are favorable to health to a much greater extent than at present. The nature of family life and of work, the two prime features of human existence, will be transformed into deliberate means of enhancing health—extending far beyond their instinctual origin. In particular, work will be converted into activity that is designed to preserve and advance the health of workers, not merely to produce goods and services. The social context of personal decisions affecting health will be recognized. An individual's choosing to smoke cigarettes is not made in a vacuum. One's milieu is a powerful determinant in such actions. Society will tend more than in the past or present to encourage its members to follow life-styles that are conducive to health. While this may sound utopian, I believe that the social achievement of approximating man's lifespan for the large majority of people will turn the social concern about health away from merely avoiding disease and premature mortality toward finding ways of maintaining health.

Finally, the realization of similar conditions of life and health for all peoples of the earth will tend to break down the present barriers to association of different people. Disparities in the conditions of life and health as well as geographic, historical, economic and cultural factors exacerbate the antagonisms between people that now take national form. Resolving such problems has become not just desirable, but essential, for mankind. While ultimately that may lead to greater homogenization of mankind, cultural differences will persist for a long time if not forever and probably be actively cultivated as a means of enhancing life for all.

Thus the trend toward better health will carry tremendous consequences for the social conditions of man's existence and how he relates to those conditions.

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Ecological Aspects of Disease and Human Populations[1]

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SYNOPSIS. This paper shows how some basic ecological themes can be illustrated, in a very explicit and quantitative way, by examples drawn from the interactions between human hosts and their infectious diseases. I first discuss the population biology of infectious diseases, showing how basic reproductive rates and density dependent limitations may be estimated. Observed cycles in the incidence of childhood infections are discussed as examples of Lotka-Volterra prey–predator cycles. Trade-offs between virulence and transmissibility in the evolution of parasite life histories are discussed in general, with the Australian rabbit–myxoma virus story as a case study. I conclude by mentioning ways in which the interplay between population density and transmission thresholds may have influenced human history.

INTRODUCTION

The work presented in this paper grew out of my interest in the possibility that parasites—broadly defined to include viruses, bacteria, protozoans and fungi along with the more conventional helminth and arthropod parasites—may regulate the numerical abundance or geographical distribution of many populations of plants and animals. The search for data to test some of the emergent ideas about the dynamics of host–parasite associations led naturally to a focus on human hosts and their infectious diseases, which understandably have been better studied than most other animal host–parasite systems.

In what follows, I shall show how some basic themes in population biology and evolutionary ecology can be illustrated by particular examples of infectious diseases of human hosts. First, I discuss the basic reproductive rates and the density dependent regulation of specific infections in human populations. Second, regular cycles in the incidence of many childhood infections are discussed as an explicit example of prey (host)–predator (infection) interactions, and interepidemic periods are shown to conform fairly accurately to the Lotka-Volterra cycle time. Third, a general discussion of the evolution of virulence is backed up by an explicit analysis of the microevolutionary trends exhibited by the myxoma virus–Australian rabbit association. Finally, I give a brief outline of some more general aspects of the interplay between disease and human history.

None of this material is new; all of it has been published before, one place or another. In this review I shall therefore try to steer a middle course, sketching material that could enrich an introductory biology course (and which may be unfamiliar to most introductory biology teachers), yet not unduly cluttering the literature with material that can be found elsewhere. In particular, I have not reproduced figures from easily accessible journals (*Science, American Scientist, Nature*), although illustrations from the less accessible *Journal of Hygiene* have been reproduced. My hope is to give just enough detail to stimulate people to turn to the primary sources.

Throughout the paper, such distinctions as are made among parasites are made on the basis of their population biology, rather than on conventional taxonomic lines. One major distinction is between *microparasites* and *macroparasites* (Anderson and May, 1979). Broadly speaking, microparasites are those having direct reproduction, usually at very high rates, within the host. As exemplified by most viral and bacterial, and many protozoan, infections, microparasites tend to be small in size and to have short generation times. Although there are many exceptions, the duration of infection is typically short relative to the average lifespan of the host, and hosts that recover

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usually possess immunity against reinfection, often for life. Microparasitic infections are thus characteristically of a transient nature. In contrast, macroparasites typically have no direct reproduction within the host, and are larger and have much longer generation times than microparasites. This category embraces essentially all parasitic helminths and arthropods. When an immune response is elicited, it usually depends on the number of parasites present in the host, and tends to be of relatively short duration. Thus macroparasitic infections are typically of a chronic or persistent nature, with hosts being continually reinfected. It follows that for mathematical models of microparasitic infection processes, the host population can usefully be divided into several distinct classes (*e.g.*, susceptible, infected, recovered and immune). For macroparasites, on the other hand, the various factors characterizing the interaction—egg output per parasite, pathogenic effects upon the host, evocation of an immune response in the host, parasite death rates, and so on—all tend to depend on the number of parasites present in a given host; this requires more complicated mathematical models that account for the distribution of parasites among hosts. The examples discussed below are mainly chosen from the world of microparasites.

Basic Reproductive Rates and Density Dependent Regulation of Microparasites

The basic reproductive rate of a species (denoted as R_0) is defined to be the average number of female offspring produced by an adult female in the absence of density dependent constraints. As most populations at most times are fettered by density dependent constraints of some kind, R_0 is notoriously hard to determine. What, for example, is R_0 for humans? Healthy Hutterite females have completed family sizes of around 11 ($R_0 = 5.5$), but they delay first reproduction until their early 20s, which suggests R_0-values as high as 7 might be attained (which would have enabled Noah's offspring to have repopulated the earth in the Biblical time scale available; this feat was a problem for Victorian Fundamentalists, for whom so high a value of R_0 seemed implausible).

For microparasites, R_0 is defined as the average number of secondary infections produced when one infected individual is introduced into a host population where everyone is susceptible. That is, R_0 is the product of the transmission rate (λ, the number of secondary infections produced per day) times the duration of infection:

$$R_0 = \frac{\lambda}{\alpha + b + \nu} \qquad (1)$$

Here $1/(\alpha + b + \nu)$ represents the duration of infectiousness: α is the disease-induced death rate, b the death rate from other causes, and ν the recovery rate; individuals move out of the infected class at a rate given by the sum of these three rates. Notice that λ will in general increase as host population density increases; there will often be a *threshold* host population density (N_T) such that the infection cannot be maintained ($R_0 < 1$) in host populations below threshold density, and can be maintained ($R_0 > 1$) in those above it.

Although R_0 for a microparasite can be clearly defined—either verbally or by eq. (1)—it cannot easily be measured directly. The mortality and recovery rates (α, b, ν) can indeed be found, but the transmission rate (λ) involves etiological, environmental and social complexities that make direct evaluation essentially impossible. The basic reproductive rate can, however, be estimated indirectly if one assumes the host population is "homogeneously mixed," in the sense that, on average, all host individuals have the same epidemiological experiences (independent of age, social class, genetic makeup, geographical location, and so on). As the infection becomes established in such a homogeneously mixed population, the basic reproductive rate must be discounted because many of the potential infectees have already acquired immunity; if a fraction x are susceptible, the effective reproductive rate (R) of the infection is simply

$$R = R_0 x. \qquad (2)$$

At equilibrium, the effective reproductive

TABLE 1. *Estimates of the intrinsic reproductive rate, R_0, for infections of human populations.**

Infection	Geographical location (time period)	R_0	Approximate value of p (percent)
Smallpox	Developing countries (before global campaign)	3–5	70–80
Measles	England and Wales (1956–1968)	13	92
	USA, various places (1910–1930)	12–13	92
Pertussis (whooping cough)	England and Wales (1942–1950)	17	94
	Maryland, USA (1908–1917)	13	92
Rubella (German measles)	England and Wales (1979)	6	83
	West Germany (1972)	7	86
Chicken pox	USA, various places (1913–1921; 1943)	9–10	90
Diphtheria	USA, various places (1910–1947)	4–6	~80
Scarlet fever	USA, various places (1910–1920)	5–7	~80
Mumps	USA, various places (1912–1916; 1943)	4–7	~80
Poliomyelitis	Holland (1960); USA (1955)	6	83

* The proportion of the population, p, that must be protected by immunization to achieve eradication is also shown. For details, and references to the sources from which the basic data came, see Anderson and May (1981).

rate of the infection will by definition be unity: $R^* = 1$ (with the asterisk denoting the equilibrium state). Thus, from eq. (2), the basic reproductive rate (R_0) and the fraction of hosts susceptible in the endemic, equilibrium state (x^*) are related by

$$R_0 = 1/x^*. \tag{3}$$

The equilibrium fraction x^* can be determined if serological data about age-specific susceptibilities are available. Even in the absence of such accurate information, a crude estimate of x^* can be made if one knows the average age at infection (A) and the average life expectancy (L): assuming everyone lives to age L, acquiring infection at age A, we have $x^* \simeq A/L$, whence

$$R_0 \simeq L/A. \tag{4}$$

Strictly, this approximation pertains to a stationary population, which is close to the truth in most developed countries. In countries with high population growth rates, eq. (4) is replaced by the more general relation (May and Anderson, 1985) $R_0 \simeq B/A$, where B is the reciprocal of the finite birth rate (thus in India, with around 40 births annually per 1,000 of population, $B = 1{,}000/40 = 25$ yr).

Table 1 catalogues R_0 for various infections. Most of these values come from serological studies, although the smallpox value rests on the rough approximation of eq. (4). The table comes from Anderson and May (1981), where a much more full discussion is given.

These values of R_0 may be used to give rough estimates of the total fraction of the population that must be successfully immunized in order to eradicate an infection. Suppose the fraction so immunized is p; then the fraction remaining susceptible is at most $1 - p$, and the effective reproductive rate is (from eq. [2]) at most $R = R_0 \cdot (1 - p)$. The infection will be unable to maintain itself if R is driven below unity, which leads to the eradication criterion

$$p > 1 - 1/R_0. \tag{5}$$

The critical fractions to be immunized are listed in the last column of Table 1. Notice that smallpox, with its relatively low value of R_0, is easier to eradicate than, say, measles, with its relatively high value of R_0.

The above discussion in general, and the values of R_0 and p in Table 1 in particular, rest on the assumption of a homogeneously mixed population. This assumption is unrealistic in a variety of ways, and significant complications can be introduced by age-related transmission rates, by genetic heterogeneity in the host population, by geographical heterogeneity in population

densities, and by other factors. The effects of these complications are reviewed elsewhere (Anderson and May, 1982, 1985). Estimates based on the homogeneous mixing assumption, however, often appear to be reasonably accurate, and certainly provide useful qualitative insights.

The purpose of this section is: (1) to indicate how the basic or intrinsic reproductive rate may be defined and actually measured for a microparasite; (2) to show how density dependent effects (in this case, depletion of the pool of susceptibles) limit effective reproductive rates below R_0; and (3) to show how these concepts have practical applications in the design of public health programs.

Infectious Diseases and Prey–Predator Oscillations

Most introductory biology courses will touch to some degree upon the propensity to oscillation that is inherent in most prey–predator interactions. At an intuitive level, such oscillatory tendencies can be understood as arising from the prey population doing well when predators are scarce, leading to conditions favoring predator population increase, leading in turn to prey populations decreasing under predator pressures, which in turn leads eventually to predator populations declining, and thence to prey population resurgence, completing the cycle. The simple models of Lotka and Volterra capture the essentials of this propensity to overshoot and overcompensation in prey–predator associations, and suggest the basic period (T) at which such systems cycle is approximately

$$T \simeq 2\pi(ab)^{1/2}. \qquad (6)$$

Here a and b are the characteristic time scales for prey population growth (in the absence of predators) and predator population decline (in the absence of prey), respectively. Whether this underlying propensity to oscillation at period roughly T is damped out or driven in stable, nonlinear "limit cycles" depends on the complicated ancillary details of the prey–predator association.

Discussion of prey–predator dynamics in elementary biology texts, or even in advanced ecology texts, draws for illustrative examples on plant–herbivore or vertebrate or invertebrate prey–predator interactions. Although rarely mentioned, host–parasite interactions (with parasite defined broadly, as above) are also embraced under the prey–predator rubric. Indeed, I will now argue that some human host–microparasite associations exhibit such cycles, with essentially the Lotka-Volterra period of eq. (6), in a way that is much more clearly understood than are the more conventional examples (hare–lynx, moose–wolf) of elementary texts.

Consider first the data. The 2-year cycles in the average incidence of measles in the U.K. and U.S.A. were noted early this century. Several recent reviews have summarized information about cycles in the incidence of measles and other childhood infections in developed countries (Yorke and London, 1973; Yorke *et al.*, 1979; Anderson and May, 1981, 1983). Figure 1 departs from the rather impressionistic analysis of much earlier work in showing the frequency spectrum (or Fourier transform) for the time series generated by weekly notifications of measles in England and Wales from 1948 to 1968. In Figure 1 the minor peak at a frequency 1 yr^{-1} corresponds to an annual periodicity in measles incidence (probably associated with annual patterns in school openings). The more pronounced peak at a frequency of 0.5 yr^{-1} in Figure 1 illustrates the above-mentioned 2-year cycle in measles incidence, which shows up clearly as the main feature in the frequency spectrum.

Consider next the theory. Soper (1929) considered his early epidemiological model a failure, because it did not give sustained oscillations. Soper's model does, however, give very weakly damped oscillations, and these oscillations are at the Lotka-Volterra period of eq. (6), appropriately modified to reflect a host–parasite association:

$$T \simeq 2\pi(A\tau)^{1/2}. \qquad (7)$$

Here A is the average host age at infection (the characteristic lifetime of susceptible "prey") and τ is the duration of infectiousness (the characteristic lifetime of the

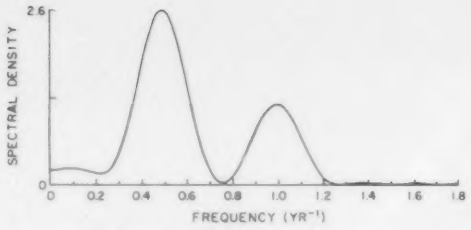

FIG. 1. Frequency spectrum constructed from the weekly measles reports for England and Wales, 1948–1968. For details of the analysis underlying this figure, see Anderson *et al.* (1985).

"predatory" infection). In passing, note that Soper's epidemiological model is superficially different from the Lotka-Volterra prey–predator model; the similarity between eqs. (6) and (7) derives from similarities in the underlying dynamical processes.

Table 2 compares the actual inter-epidemic periods observed for measles, pertussis (whooping cough) and mumps with the periods estimated by substituting the appropriate values of A and τ into eq. (7). The agreement between the observed periods and the crude theoretical estimates is encouraging. These and other results for periodicities in the incidence of microparasitic infections are discussed more fully elsewhere (Anderson and May, 1981, 1983, 1985; Anderson *et al.*, 1985).

To many pure mathematicians, the above discussion may be unsatisfactory. Although Soper's model and refined versions of it (Anderson and May, 1983) may exhibit inter-epidemic oscillations at the observed periods, these oscillations are damped. Various mechanisms—stochastic fluctuations in the input of new susceptibles by birth or immigration, seasonal variations in transmission rates, or (possibly, though not yet proved) age-specific changes in transmission rates—can "pump" the system in a nonlinear way, to produce sustained oscillations. To the pure mathematician, the focus is often on determining exactly which mechanism drives the sustained cycles. To the biologist, the essential point may be that host–parasite dynamics tend to produce cycles (sometimes damped, sometimes sustained) whose period is given by eq. (7), independent of the details.

The basic propensity for host–parasite associations to oscillate can manifest itself in a different way, with interesting practical consequences. Suppose we implement an immunization program, with the long-term aim of reducing the incidence of a particular infection, or even of eradicating it. Such a program represents a perturbation to the host–parasite system; the system is unlikely to move smoothly and monotonically to the new final state, but rather is likely to exhibit pronounced oscillations en route to this state. Figure 2a illustrates this phenomenon: the y-axis shows the number of cases of congenital rubella syndrome, CRS (taken to be proportional to the number of women contracting rubella—German measles—in the first trimester of pregnancy) as a function of the number of years after initiating a program of immunizing either 20% or 80% (as labelled in the figure) of all 2-year-old boys and girls; the number of cases of CRS is shown as a ratio to the annual number before any immunization. At 80% coverage, there are violent oscillations (with an approximate 10-year period) in the incidence of CRS, which damp to a lower level on a time scale too long to be seen in Figure

TABLE 2. *Estimates of the average duration of infection (τ), the average age at infection (A), and the predicted inter-epidemic period (T from eq. [7]) for childhood infections in England and Wales in the period 1960–1970.**

Infection	Duration of infection (days)	Average age at infection (years)	Inter-epidemic period (years)	
			Predicted	Observed
Measles	12	4–5	2.3–2.5	2
Pertussis (whooping cough)	25	4–5	3.3–3.6	3
Mumps	19	6–7	3.5–3.8	3

* The observed inter-epidemic periods are also given. (From Anderson *et al.*, 1985.)

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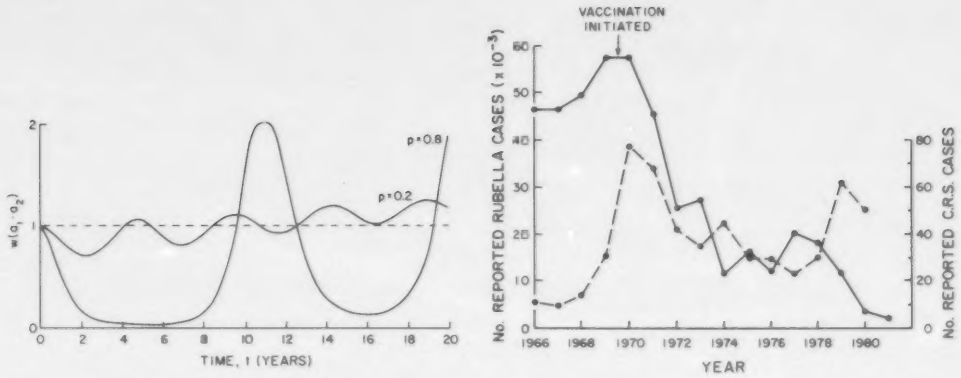

FIG. 2. a. This figure is based on relatively simple epidemiological models, and shows the temporal trends in the number of cases of congenital rubella syndrome, CRS, as a function of the number of years after implementing a program of immunizing either 20% ($p = 0.2$) or 80% ($p = 0.8$) of all boys and girls at age 2 years. The predicted incidence of CRS is displayed as a ratio to the incidence before any immunization, $w(a_1, a_2)$; at all times the incidence of CRS is assumed proportional to the incidence of rubella among pregnant women between the ages of $a_1 = 16$ years and $a_2 = 40$ years. For discussion, see Anderson and May (1983). b. Reported cases of rubella (solid line) and CRS (dashed line) in the USA between 1966 and 1981 (from Anderson and May, 1983).

2a. Figure 2a represents a ludicrous oversimplification of the real immunization program in the U.S.A.: it is based on an excessively simple model, and it neglects both immunization of adult women as part of post-natal care and other realistic complications. Figure 2a does, however, capture the major feature of the actual incidence of CRS in the U.S.A., as shown in Figure 2b. For the data in Figure 2b, notice that the incidence of CRS at first fell after immunization was begun in 1970, but that—as suggested by Figure 2a—CRS rose back almost to the pre-immunization level about 10 years later in 1979. In the absence of the theoretical understanding developed above, this upswing in the incidence of CRS shown in Figure 2b could be mistaken as deriving from a failure in vaccine production or some other extrinsic cause, rather than being recognized as intrinsic to the dynamics of the system. (Fig. 2b also shows the total number of cases of rubella, as distinct from cases in pregnant women; for total incidence of rubella, the oscillatory pattern is much less marked both in practice and in theory.) The results in Figures 2a and b are abstracted from Anderson and May (1983), where they are discussed in detail.

A more general examination of the dynamics of host–parasite associations reveals a wide spectrum of possible behavior, ranging from stable equilibria through sustained cycles to "chaos" (apparently random dynamics generated by purely deterministic equations). For example, consider an insect population with discrete, nonoverlapping generations that is regulated by a lethal pathogen which spreads in epidemic fashion through each generation before reproduction. This system exhibits purely chaotic behavior, with no stable point and no stable cycles (May, 1985). In short, host–parasite systems are capable of exhibiting a wider range of interesting dynamical behavior than is indicated by the above discussion of Lotka-Volterra cycles.

The purpose of this section is: (1) to show how the basic ideas about prey–predator cycles are borne out by periodicities in the incidence of childhood infections of humans; (2) further to show that such periodicities can be documented in detail (Fig. 2) and estimated by simple theory (eq. [7] and Table 2); and (3) to observe that such oscillations can have practical implications for immunization programs (Fig. 2a and b).

EVOLUTION OF VIRULENCE

As reviewed elsewhere (Levin and Pimentel, 1981; Levin *et al.*, 1982; May and Anderson, 1983), most discussions of host–parasite associations assert the coevolutionary pressures to be such that "successful" or "well-adapted" parasites are relatively harmless to their host. On empirical grounds, this assertion may be supported by the observation that most of the spectacular examples of havoc wrought by pathogens are for newly introduced species of plants or animals, or for pathogens introduced into a new region. On theoretical grounds, the argument is often advanced that it is for the good of both host and parasite species for hosts to be relatively unharmed by infection.

A more careful appraisal of these arguments leads to a more equivocal conclusion. Many parasites—from viruses to helminths—enhance their transmission rates by modifying the behavior of primary or intermediate hosts, often in ways that are conspicuously deleterious to the host (for a recent review, see Moore, 1984); the lethal damage done to the central nervous system by rabies virus, for example, seems ineluctably entwined with the biting and other behavioral changes whereby the infection is transmitted. Setting aside parasites that modify host behavior, there are many long-established pathogens for which high lethality seems to be associated with effective transmission: the various baculoviruses, which kill their insect hosts and effectively turn them into masses of viral transmission stages, are examples. In humans, the virulence of smallpox (death in 20–30% of all cases) does not appear to have diminished over the roughly 1,000 years for which we have records (Fenner, 1983). The theoretical arguments for the evolution of "harmlessness," moreover, are often unabashedly group selectionist. While it may indeed be best for the parasite population not to harm hosts too much, the workings of natural selection are usually such that a "nasty" mutant strain will take over if it produces more progeny, even at the expense of greater harm to hosts.

The theoretical part of these arguments can be illustrated by returning to eq. (1), which shows how (in the simplest case) the basic reproductive rate of a microparasite (R_0) depends on the disease-induced death rate or virulence (α), recovery rate (ν) and transmission rate (λ). If these epidemiological parameters are entirely independent of each other, then clearly R_0 is maximized by having α tend to zero, corresponding to a harmless or avirulent parasite. But often the pathogenic effects of the parasite (as ultimately measured by α) are intrinsically associated with the production of its transmission stages, so that λ, ν and α are intimately dependent on each other. Once these trade-offs are acknowledged, it appears that many different coevolutionary paths can be followed, depending on the nature of the interplay between virulence and transmissibility for a specific parasite. In particular, if it were to happen that λ were a faster than linear function of α, the evolutionary pressures on the parasite would be toward ever increasing virulence.

For a clearer understanding of the evolution of virulence in any one host–parasite system, we ideally need information about the relations among virulence, transmission rate, recovery rate, and the cost of resistance in the host, for different genotypes of host and parasite. Such information is very rarely available.

The introduction of myxoma virus into wild populations of rabbits in Australia and Britain in the early 1950s does provide one unusually well-documented and interesting case study. The viral strain that was first introduced was highly virulent, but over the next few years successively less virulent strains of the virus appeared. From the carefully gathered data in Australia (where field strains of virus were monitored against the original genotypes of rabbits kept in the laboratory for reference, and where rabbits from the field were similarly checked against reference strains of virus), it is possible to get rough estimates of the way λ and ν depend on α for this system. Thence, via eq. (1), the overall relation between R_0 and α can be assessed for the myxoma–rabbit association. The technical details of this analysis are outlined

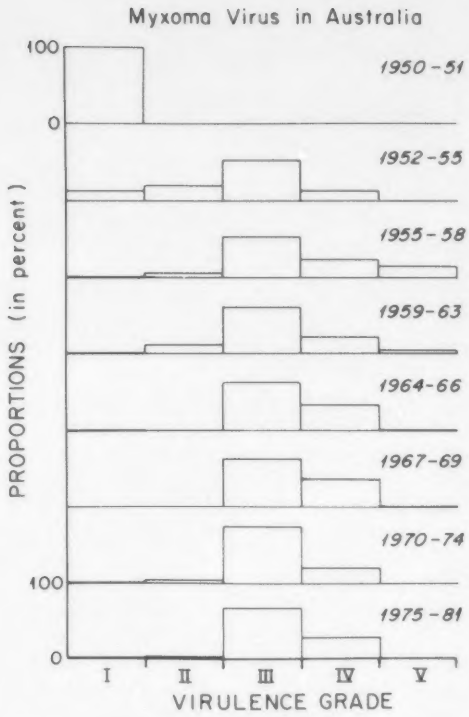

FIG. 3. This figure shows the proportions in which the various grades of myxoma virus have been found in wild populations of rabbits in Australia, at different times from 1951 to 1981 (from May and Anderson, 1983, based on data compiled by Fenner, 1983).

elsewhere (May and Anderson, 1983). The conclusion is that R_0 is maximized by an intermediate grade of virulence: relative to the optimum strain, more virulent strains kill rabbits too fast, while less virulent strains enable rabbits to recover too fast.

The outcome of this theoretical exercise is roughly in agreement with the data, which are displayed in Figure 3. It will be seen that, following the introduction of highly virulent strains ("grade I") in 1950–1951, there rapidly appeared a series of successively less virulent strains (II–V). By 1952–1955 the predominant strain of virus found in the field was one of intermediate virulence ("grade III"), and this situation has persisted essentially unchanged over the subsequent three decades. A broadly similar (though less thoroughly documented) history has been followed in Britain, despite significant differences in the ecology of the myxoma–rabbit association (in Britain the intermediate vector is a flea, in Australia a mosquito). Note that Figure 3 is at variance with the story told in several introductory biology texts, which assert the virus to have steadily and systematically declined in virulence. For a more full discussion, and background references, see May and Anderson (1983).

(More generally, the evolution of resistance to pesticides by an increasing number of agricultural pests and disease vectors provides many examples where microevolutionary processes can be studied in detail. It is possible to use elementary population genetics to make rough estimates of the time taken for resistance to appear, as a function of the initial frequency and degree of dominance of the resistance gene and the generation time of the pest. The estimates, moreover, are in good agreement with observed patterns. Such case studies could replace the canonical example of industrial melanism in the peppered moth in introductory biology courses, with the advantage of their being both fresh and of demonstrable practical interest. For a recent review of this subject from the above viewpoint, see May and Dobson [1985].)

The purpose of this section is: (1) to show how evolutionary processes involve explicit trade-offs (in the case of microparasites, between virulence and transmissibility); (2) incidentally to stress that selection usually acts on individuals, not on groups; and (3) to discuss the myxoma–rabbit association as an example of microevolution (and to suggest other examples from the world of pesticide resistance).

DISEASE AND HUMAN HISTORY

Microparasitic infections are typically of short duration, and infected hosts either die or recover to an immune state. It is thus usually necessary to have a large population of hosts, in order that the population of susceptibles be replenished by births at a sufficiently high rate to keep the microparasite ticking over within the population. In other words, the threshold density for a host population to be able to maintain a

directly transmitted microparasitic infection is usually high. To the contrary, macroparasitic infections are typically long-lasting, and are characterized by continual reinfection; macroparasitic infections can maintain themselves endemically within relatively small populations of hosts. As discussed by Anderson and May (1979), these observations suggest that directly transmitted microparasitic infections are characteristically more common among organisms that exhibit herd or schooling behavior, or that breed in large colonies, while macroparasitic infections are characteristically more significant for relatively solitary animals. Some anecdotal support for these ideas comes from the observed abundance of directly transmitted microparasitic infections within modern human societies, large herds of ungulates, breeding colonies of seabirds, and communities of social insects; there remains, however, much need for comparative studies in which data are systematically compiled.

For humans, it is estimated for example that communities comprising 300,000 or more people are needed to maintain measles as an endemic infection. Such population densities simply did not exist in pre-agricultural days. It is widely believed that the directly transmitted microparasites responsible for much mortality in historical times—smallpox, measles, cholera, and the like—could not have been present in human populations before advent of the Agricultural Revolution some 10,000 years ago; the population densities in hunter–gatherer societies are well below the estimated thresholds for such infections. These ideas have several implications for the broader patterns of human history.

First, it is recognized that the Western European conquest of the New World and Oceania was accomplished largely with biological weapons: smallpox, tuberculosis, and measles (McNeill, 1976). Recent work suggests the native populations in North and South America were typically reduced to 5% of their pristine abundance immediately following contact with Europeans, and sometimes even before such contact (as infectious diseases were carried ahead of the human invaders, along trade routes); for a review, see May (1984). But why was this situation not symmetrical? Why did the New World people not reciprocate against the Europeans with their own particular infections to which Europeans lacked resistance? The answer is surely that the inhabitants of the New World and Oceania had no similarly virulent microparasites of their own with which to counter because they were, or until recently had been, at densities too low to maintain such infections. A notable exception that may have been exported to the Old World (although even this is debatable) is syphilis, which is well adapted to persist at low host densities.

Second, and on a grander scale, consider the sweep of demographic history over the past 10,000 years or so. It is often thought that this history is one of steadily increasing population growth, with a few fluctuations (associated with events such as the black death in Europe or famines in China) superimposed. This is not so. According to Deevey's (1960) necessarily rough estimates, the first 5,000 years after the beginning of the Agricultural Revolution saw human numbers increase from about 5 million to about 100 million. A second, roughly equal period, from about 5,000 years ago to around 300–400 years ago, saw a slower rate of increase to approximately 500 million. That is, in the first half of the 10,000 year span since the beginning of the Agricultural Revolution human numbers increased by a factor 20, and in the second half by a factor 5. There are several possible explanations for this diminution in average population growth rates, but I believe the most likely explanation is that during this time human conglomerations rose to levels capable of maintaining directly transmitted microparasitic diseases, whose effect was then to slow population growth.

Third, it should be emphasized that even today age-specific survivorship curves are very different in developed countries from those in developing countries, with the higher mortality rates in the latter countries being unambiguously associated with the combination of infectious diseases and malnutrition. These facts are discussed further (with background references), and

illustrated by a dramatic figure, in May (1983; see Fig. 9 in that paper). Mortality and morbidity produced by infectious diseases continue to be a major factor for most people today, as they have been for at least the past 10,000 years.

The purpose of this section is: (1) to show that parasites—broadly defined—play an important role in human demography; and (2), in particular, to show how the interplay between population density and transmission thresholds for many microparasitic infections helps explain some major features of human history.

CONCLUSION

My paper has concentrated on four distinct topics, showing how specific aspects of the interactions between human hosts and parasites can illustrate basic ecological themes. These set pieces have intrinsic interest; many students find material more engaging if it involves humans rather than other animals (nor can I, in view of the way I have chosen my set of topics, criticize such narcissism). Beyond this, the examples also serve the constructive purpose of showing that humans, like all other animals, obey the basic principles of population biology and evolutionary ecology.

ACKNOWLEDGMENTS

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Man and the Sea—The Ecological Challenge[1]

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SYNOPSIS. Cultural "revolutions" are characterized by increased utilization of natural resources, resulting in increased carrying capacity for the human species. We are witnessing the *Marine Revolution*, which challenges us to develop unifying, ecosystem-based approaches to the science and use of the sea. *Knowing* (*i.e.*, science) marine processes should form the fundamental basis for *doing* (*i.e.*, conservation and management), within a global human ecological framework.

The issues of human ecology are about the same by land or sea, but these subdivisions of Earth are fundamentally different. The sea must be understood in its own right, rather than be driven by terrestrially-derived models. For example, animal diversity is on a species level by land; marine diversity is at higher taxonomic levels and, if viewed functionally, is greater than the land's. This has important implications in the design of protected areas. Another example concerns the roles of large organisms in ocean processes; fishery ecology has been neglected, but a total ecosystem viewpoint is essential towards placing fisheries on a sustainable basis.

New perspectives toward the sea are rapidly emerging. Satellites have the potential for revolutionizing oceanography. Ecotoxicology is in the process of addressing pollution on an ecosystem basis. A unified scientific perspective of "oceanology" is required to help meet problems of human ecology during the Marine Revolution.

> Roll on, thou deep and dark blue ocean,—roll!
> Ten thousand fleets sweep over thee in vain;
> Man marks the earth with ruin,—his control
> Stops with the shore . . .
>
> George Gordon, Lord Byron
> From: *The Sea, Childe Harold's Pilgrimage*

The mystique of the sea is still with us. Ever-growing fleets continue to dominate man's economic use of the sea—as a surface for commerce and power. Lord Byron observed the wreckage being made of the land; he could not have observed similar impacts on the sea. Science struggles to detect such impacts today. But despite the power of technology, we cannot "control" the sea, as is the case for the bulk of the land. Our culture is pre-Agricultural Revolution there—that of the hunter-gatherer, depending on natural processes for its provender. But times are changing—fast.

This is the time of the *Marine Revolution*. Revolutions, such as the Agricultural and Industrial, mark major shifts in culture which result in vast leaps in carrying capacity—for us, but often at the expense of companion species on this planet. This has happened largely because of man's increased ability to domesticate, manipulate, and control his environment. John Moore (1985), in his comprehensive review of our theme, states: "The two most important characteristics of the human species that have made civilization possible have been the ability to domesticate plants and animals in order to ensure a more reliable supply of food and the ability to use sources of energy other than food to perform work." Even now, these abilities largely stop at the shore.

Revolutions are also characterized by accelerated rates of cultural change. Nevertheless, they are hardly observed when they are happening. As I have noted earlier (Ray, 1970): "The Marine Revolution is, to my mind, quite as important a development as the previous Agricultural and Industrial Revolutions. It is no more obvious on a day-to-day basis than [they] were in their time. Future Man will clearly see this Revolution as his inner-space logistics and utilization increase."

Institutions exhibit extraordinary inertia in adapting to change, particularly "revolutions" longer than a human lifespan, and hardly perceptible to any one human

[1] From the Symposium on *Science as a Way of Knowing—Human Ecology* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1984, at Denver, Colorado.

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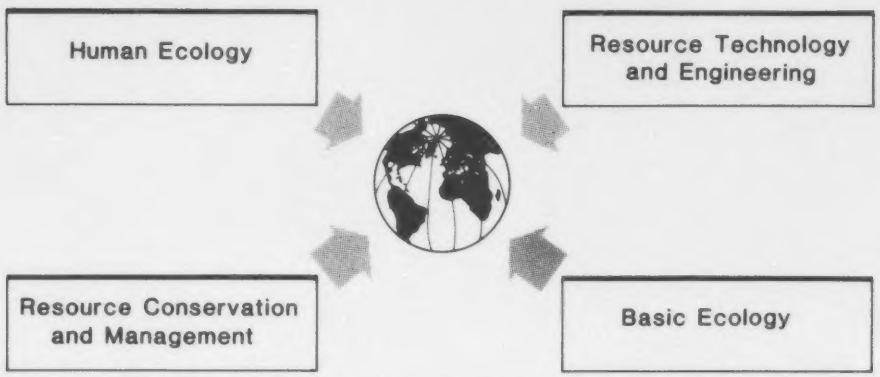

FIG. 1. The inter-relationships of aspects of environmental science. After McCormick and Barrett (1979).

being. This includes teaching institutions, and, despite the need, "human ecology" barely makes it to academe: its companion, "environmental science," is not well defined as a single discipline. A start has been made by the definition of "Ecoscience," as Ehrlich *et al.* (1977) put it. McCormick and Barrett (1979) have conceived environmental science in four interrelated parts, which I have adapted in Figure 1. A very few college curricula teach by this model, fewer in marine science than in terrestrial science; so-called "marine affairs" programs could possibly close this gap, but they are presently stepchildren of "hard science" institutions. As I see it, human ecology is the dominant aspect of environmental science. Figure 2 suggests that ecology and economy are its two interacting features, taken in their Greek originality—"understanding" and "management." The question is: how do we achieve them? The answer to this question is mostly outside the scope of this paper. But, certainly, teaching must be a basis for a solution.

Mayer (1984) told the first of these symposia: "We must discontinue teaching science as if it is a self-contained discipline existing of, by, and for itself. Instead, we must begin to understand and to communicate the relationships between science, technology, and society." This is essential for the sea, as the Marine Revolution is largely driven by a perceived economic necessity for continued growth, with the lawyers and politicians having become its managers and, to a good extent, its prophets. The reasons for this are historical and perceptual. Man is mostly physically and mentally removed from the sea and, except for the sea's mystical appeal, the bulk of humanity takes an out-of-sight, out-of-mind attitude, despite the fact that over half of us the world over live in the "coastal zone."

The challenge of the Marine Revolution is to place the science of knowing the sea within a human ecological framework. This is a forbidding challenge, squarely to be confronted by those of us that teach. Scientists have the task of providing the basis for decisions about how man explores and exploits the sea. Do our curricula provide the basis for such leadership? Moore (1985) makes the observation: ". . . many courses and textbooks tend to be fact-ridden encyclopedias testing the student's ability to survive rather than providing a deep and

satisfying understanding of the natural world." This is surely true for most oceanographic and fisheries texts that I know (treatments in marine biology seem more refreshing—possibly a result of my own bias). This is to say that the texts themselves seem to present formidable obstacles to development of either unifying concepts for "oceanology" or for evolving a "human ecology" of the seas. Throwing facts at problems, or at students either, is hardly satisfactory—as much as we need good facts to bolster our arguments.

ISSUES AND DIFFERENCES

Ray and Norris (1972) have called the sea "a bouillabaise of animals and plants, of uncountable microorganisms, of nutrients, of degradation products of life, of inorganic contributions from land, from chemical precipitation, and of dust from the atmosphere. Its 'winds,' which are the ocean currrents, move at all levels from the surface to the deepest sea . . . . With them move nutrients and life. With them move clouds of reproductive products, and of larvae, so that no part of the sea is ever free of the replenishing supply of life suited to it, save those places where man has so altered the conditions of life that occupancy is not possible." The first issue, then, is *knowing* this bouillabaise; the second is *doing* with what we know.

There can be little doubt that the sea is a different place than the land to which we giant, air-breathing, warm-blooded, land animals have adapted. Nevertheless, the issues with which we must deal are about the same: the stress of pollution and the capacity of ecosystems to sustain themselves in face of human insults; the assessment and management, or protection, of species and the maintenance of biological and ecological diversity; the management of areas, especially those deemed "critical habitats," for productive or endangered species; the maintenance of the ecological processes that sustain all life, including ourselves; and, of course, the sharing of our knowing, which we call "teaching."

Complete issue identification would require whole library shelves. I can do no more than summarize from two recent documents. First, DOSP & CEPLA (no date) have identified five areas of environmental concern contained in the 1982 United Nations Convention on the Law of the Sea: (1) conservation and management of living resources, (2) pollution prevention, reduction, and control, (3) transit management, (4) environmental management of other activities in accordance with "sound principles of conservation" (*e.g.*, the control of pollution from land-based sources and ocean dumping), and (5) other general matters, such as coastal state jurisdiction within the exclusive economic zone (EEZ) and scientific research. The Convention is complex and controversial, but at least, it offers hope for confronting the "tragedy of the [ocean] commons" (see Hardin, 1968). That the United States has not signed this Convention hardly speaks well for the maturity, wisdom, foresight—or unselfishness—of those currently handling the matter.

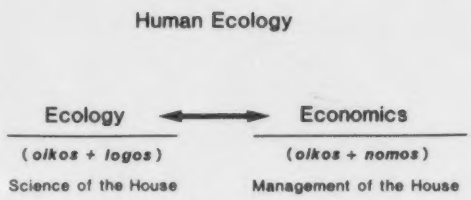

FIG. 2. Relationships in human ecology.

Second, Bliss-Guest and Keckes (1984) summarize the United Nations Environment Programme's efforts within "regional seas." In contrast to the Law of the Sea, which is concerned with non-territorial seas and those areas outside the EEZs, this program places emphasis on national cooperative efforts within specified regions (*e.g.*, the Mediterranean or the Caribbean). Again, five areas are identified, within an "action plan": (1) environmental assessment, (2) environmental management, (3) environmental legislation, (4) institutional arrangements, and (5) financial arrangements. Each of these presents an issue to be solved, whether biological, ecological, institutional, legal, or economic.

I do not intend to proceed to national or local detail. These two references should

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suffice to illustrate the scope of the problems involved. To boil it down a bit, there are two major environmental concerns—living resource utilization and pollution. As the marine bouillabaise grows thicker with men, machines, and wastes, the essential role of ecologists is to provide the scientific basis for problem solving. However, we must face the fact that marine science is at least a century behind land science in grappling with the burden we must accept; furthermore, problems rapidly seem to multiply beyond our capacity even to study them, much less to arrive at solutions.

To face this mandate, we must first learn to "think wet." The most striking factor is that the logistics of marine science are burdensome and expensive; they are also horribly clumsy. Further, not one of our senses is really adapted for investigation of things much beyond our touch within the aqu. ic medium. Even our sight is largely worthless without a mask; have you ever tried to smell or taste underwater? Fishes have other, more efficient senses to allow perception of events in their dense world. Therefore, almost all that we do by sea requires technology and the risks that placing machines between the observer and the observed involve. This increases costs as well. Recently, I was informed that to fulfill our desire to test a hypothesis that walruses have a sort of "mobile lek" reproductive social structure would cost about $3 million in ship time! At such a cost, will we ever know?

Pielou (1979) summarizes the major features of the sea by noting that: (1) vegetation does not form a structured environment, except close to shore, (2) the oceans are contiguous and species generally have large ranges, (3) boundaries to dispersal are subtle, the more so the farther to sea, (4) latitudinal zonation is more marked, and (5) the oceans are three-dimensional. All of these are in strong contrast to the land, yet most of our management procedures are biased by being land-derived; traditional concepts of "ownership" rather than the "stewardship" inherent in emerging Law of the Sea are prime examples.

Moore's (1985) essay brings other differences to mind. First, he reminds us that no land animals are sessile, but water moves food and reproductive products, so many marine forms can afford to stay put. Second, he notes the great biological diversity and abundance of the tropics, and that the polar regions are far less so. This is not entirely true by sea; polar seas are not as diverse in species (see below), but their biomass mostly exceeds the tropics. There are several reasons for this; a major one concerns the relatively constant medium of sea water and how nutrients are handled in marine systems. Moore also tracks the domestication of animals and plants terrestrially; I have noted above that domestication of the sea is a future dream.

A few more differences should be noted. Marine ecosystems are by no means as uniform as we formerly suspected. Ehrlich *et al.*'s (1977) assessment that "considering their size, the oceans are an extraordinarily uniform environment" underestimates the texture we can perceive within its space and the habitat diversity that we are only beginning to discover. Even so, marine ecosystems *are* very big! William Rose Benét, in his poem, *Whale,* provides an appropriate image:

> Ocean, wherein the whale
> Swims minnow-small

These differences, taken together, have several implications. A fundamental implication for environmental science is that resources and environmental issues are *shared* among nations. This is a feature for which our political, economic, and scientific institutions are only primitively equipped to cope. In contrast is the significant difference of human perception. The sea holds considerable mystique and the largest of earth's creatures—the whales—have even been assigned almost human properties, some of which flatter neither them nor us. Nonetheless, much of this mystique is fortunate, for it creates within us a matrix for caring, wondering, investigating, and teaching. I am reminded of a tale about two persons first seeing the Pacific Ocean from the Golden Gate. The first was awed, as we all have been by the majesty of the scene, and is reported to have said: "Look at all that water!" Only

to be reminded: "Yes, but think, that's only the top."

CASES

Two examples will serve to associate fundamental ecological concepts with present human activities. Each begins with a hypothesis. The hypothesis is neither the only nor, necessarily, the best of all possible hypotheses that may be stated for the case. The examples were chosen by means of three criteria: (1) an important ecological concept is involved, (2) a human use or impact is important to resources or the environment, and (3) the resulting conflict presents a major management challenge.

Class 1. Diversity and protected areas

Hypothesis. Diversity is functional, as well as taxonomic, and involves both life forms and habitats. Maintenance of biological and ecological diversity depends on a range of protected area types, chosen on the basis of their ecological representativeness.

Discussion. Hutchinson (1959) in his classic "Homage to Santa Rosalia" states: "The marine fauna although it has at its disposal a much greater area than the terrestrial, lacks this astonishing diversity. If the insects are excluded, it would seem to be more diverse . . . . The extraordinary diversity of the terrestrial fauna, which is much greater than that of the marine fauna, is clearly due to the diversity provided by terrestrial plants." Hutchinson was referring to diversity on the species level, and there is no arguing the fact that, of perhaps 10 million species in the world, the sea contains only about 20%. This is only one way of looking at things, however.

One might ask: what are the comparative diversities of different taxa of the land and sea? Figure 3 presents a comparison for animals only, and illustrates that at the species level the land is 4 times more diverse than marine environments, but at the Class and Phylum levels, the sea is perhaps 20 times the winner. This is due to the fact that all phyla are present in the sea and the bulk of classes are exclusively marine; some of these are represented by a very few species indeed. Furthermore, Hutchinson points out that metaphoetesis is common

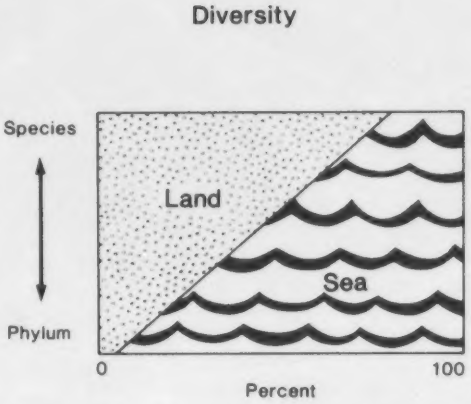

FIG. 3. Comparison between diversity of land and sea at different taxonomic levels.

in fishes; that is, differences in size (*e.g.*, schools of herring of different cohorts) allow one species to occupy several niches. If we carry this idea further to the invertebrates, we soon find that each life history stage acts as if it were a separate species and many invertebrates have a half dozen or so of these from larva to adult. So, from the ecological-functional point of view, the concept of diversity extends beyond the taxonomic, species restraints into which it is most often simplistically placed.

Let us go a step further. Taxa and life forms are almost always described as nouns. Suppose we looked at them as collections of verbs, which after all, each of us really is—where would we be without eating, breeding, lecturing, etc.? The totality of such functions describes "niche." Furthermore, each life form's functions occur at some place during some time: we call these places "habitats." We may now ask: which of these habitats is essential or "critical" to the species' survival and how are those habitats maintained by ecological processes? That is to say that species/life form diversity is inextricably mingled with habitat diversity.

Where does this place diversity and the contrasts between land and sea mentioned by Hutchinson? Obviously, diversity is no simple matter. One could, merely on the basis of the number of life forms of most

marine invertebrates and fishes expand marine diversity to equal the land's. Is this an unfair ploy? I think not, for the following reason. All life forms of a species, and the critical habitats of each, must be maintained in order to maintain both that species and its community structure, and this principle is as true by sea as by land. Related to this is whether ecosystems can survive without their dominant or "keystone" species. This probably depends on the importance of the species to essential ecosystem processes and how one chooses to define "ecosystem"; that is, one must ask whether ecosystems are fundamentally altered with or without the presence of particular species. For example, is the Southern Ocean the same ecosystem now that the great whales of the genus *Balaenoptera* are so few, their niches now presumably occupied by penguins and seals?

That these are not idle matters is exemplified by conclusions of the Department of State (1982): "the preservation of genetic diversity is both a matter of insurance and investment." This is to say that diversity has risen from science to policy. It is also important to recognize that this policy can only be addressed through application of some very fundamental scientific concepts.

This brings me to the second part of my hypothesis, that diversity may be best maintained through a system of protected (or conserved or managed) areas. There is a large and growing literature on protected area concepts which space forbids examining here. Reference might be made to the recent World Conference on National Parks and to the Introduction to the resulting volume by McNeely (1984) who says: "national parks need to be supplemented by a wide range of other sorts of protected areas which can help meet the social and economic needs of modern human society." The challenge here is: by which biological, ecological, and human criteria are protected areas, in all their necessary array, to be chosen?

There are many criteria, but I have space only for a brief examination of the criterion of "representativeness." The thesis is that protected areas should "represent" all ecological types and their included biota. Theories of island biogeography initiated much of the application of this criterion, and continue to do so. For the land, Udvardy's (1975) classification scheme has been widely applied. For the sea, no similar system has been available, specifically addressed to the selection of protected areas. Consequently, the International Union for Conservation of Nature and Natural Resources recently supported Hayden *et al.* (1984) for development of a method to show how physical oceanic and meteorologic features, combined with coastal biotic provinces, can be used to classify marine environments. Figure 4 illustrates our scheme for the Indonesian Region. The scale is very large (in cartographic terms) and the notion is to apply the same sorts of methods to smaller areas in order to arrive at a comprehensive and internally consistent system for the world's coasts and oceans.

Thus, for diversity maintenance, it appears obvious that some challenging scientific concepts must be utilized. Starting from simplistic concepts of biological species diversity, we soon find that descriptive units, such as taxa, are not enough. This takes us into descriptions of life history stages and into the processes that support each of them. Soon, we find ourselves immersed in problems of classifying environments.

Before leaving this case, allow me to bring up one final point. Where does the "coastal zone" fit into our land-sea clssifications? To this broad belt, from coastal plains to the continental slope, many species have adapted. Both by land and sea, productivity is high; about 99% of the world's fish is caught within it. Is the coastal zone an ecotone or an ecosystem in its own right? Where do the tidal pools and the mangroves belong? Do we live on a tripartite planet—land, sea, and coastal? We must leave this for another day.

Case 2. Ecosystems and large organisms

Hypothesis. Large organisms of the sea, upon which man depends for fisheries, exert "controls" over both community structure and nutrient flux. In order that ecosystem functions can become under-

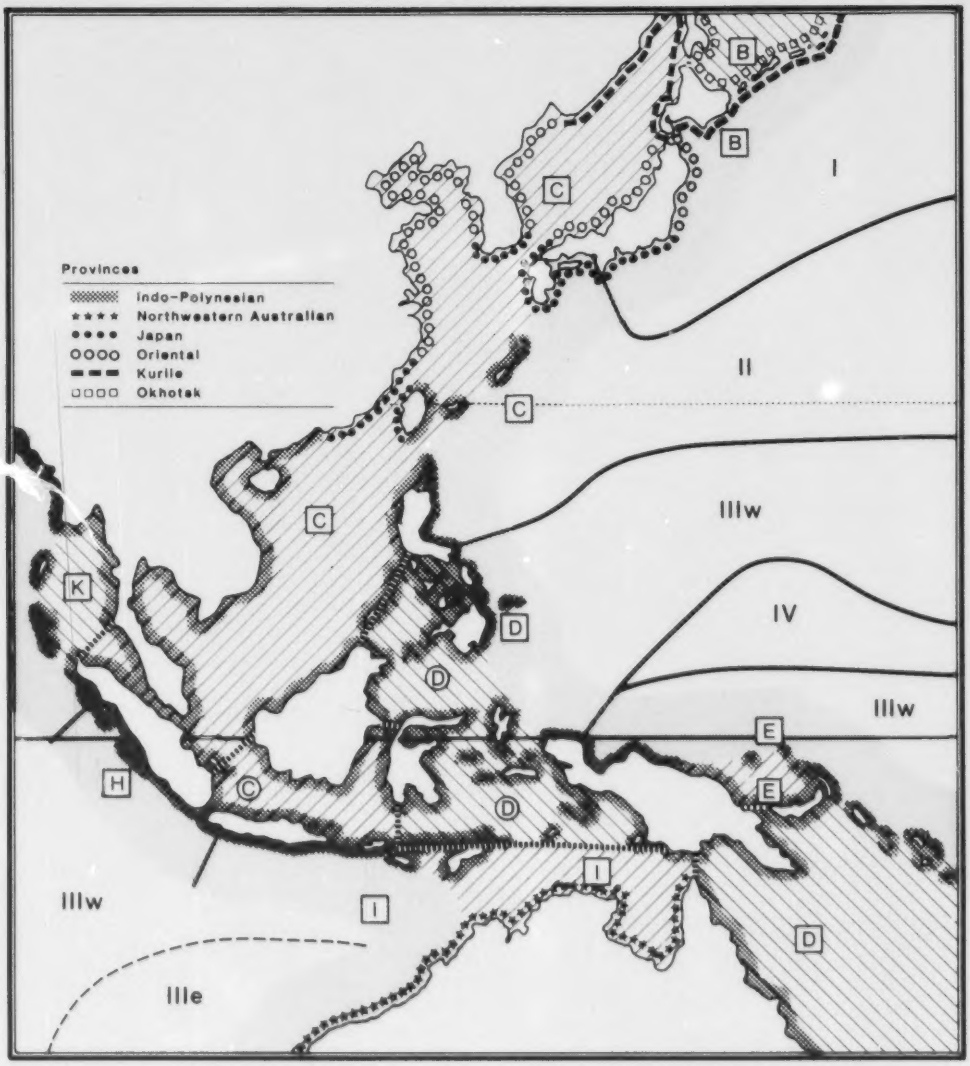

FIG. 4. A proposed classification of coastal and marine environments for the Indonesian Region. Ocean Realms are expressed by Roman numerals. Marginal seas are cross-hatched, and faunal provinces are expressed as lines of dots. See Hayden *et al.* (1984) for full explanation.

stood and that fisheries can become predictable and sustainable, research and management must be placed on an ecosystem basis.

Discussion. Not so long ago, the world ocean was thought to be virtually inexhaustable. Fisheries continued to expand, interrupted only by war, until about a decade ago when the world catch stabilized at about 70 million metric tons. Today, it shows signs of decline; certainly it has become less and less predictable and, thus, less and less economically viable. But our older ways still dominate; the superabundant, little crustacean called "krill" (*Euphausia superba*—the "haughty good-

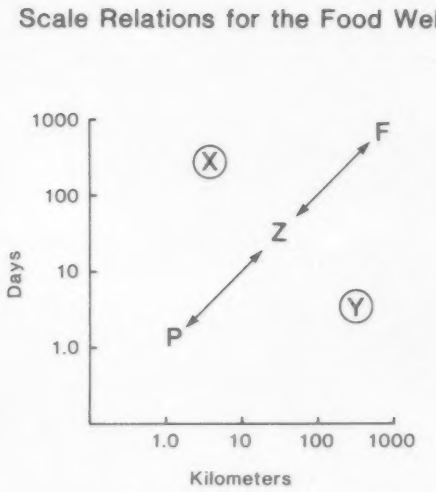

FIG. 5. Scale relations among phytoplankton (P), zooplankton (Z), and fishes (F). See text for explanation. From the Ocean Science Board, 1980.

shining one," in its Greek definition) of the Southern Ocean is sought to "solve" the world fishery dilemma. As Ehrlich *et al.* (1977) put it: "Perhaps the most pervasive myth of the population-food crisis is that humanity will be saved by harvesting the 'immeasurable riches' of the sea."

What has made fisheries so unpredictable and unstable? Is this the natural course of events in marine ecosystems? Possibly—but, probably also, it is our understanding, as well as our overfishing, that is at fault. The Ocean Science Board (1980) has pointed out that generalities such as "health of the ecosystem" and "maximum productivity"—as stated in much law and policy—are insufficient. Also, serious limitations of "yield" theory, by which most fisheries still are managed, including those for whales, have become obvious. New scientific approaches are required and management must be based on close cooperation among ecologic, economic, and social forces; this, by definition, must involve a wide array of disciplines from physical oceanography to theoretical ecology. Specifically, fisheries models have been deterministic, but they must become stochastic, taking ecosystem processes into account. A most dramatic recent example is the El Niño event that altered fishery patterns over almost the entire Pacific and even beyond; patterns of fish distribution were altered, and so was fishing.

Recruitment has been singled out as one of the most important factors for investigation and the Ocean Science Board has presented a most interesting model of the time and scale characteristics of phytoplankton, zooplankton, and pelagic fish (Fig. 5). Phytoplankton exhibits short-term biological features (*e.g.*, life-span, migrations) within small areas (*e.g.*, limited areas of "patchiness"); oceanic fishes exhibit generally long life and migrate over huge ocean areas. Zooplankton is somewhere in between. This simple concept is complicated by the fact that small scale, permanent or predictable areas of ocean exist (*e.g.*, fronts) where fishes aggregate (area X); others are strongly influenced by short-term events that may affect large areas, such as storms and shifts in circulation patterns (area Y). The Ocean Science Board then examines the nature of our research and concludes that: "At present much of our work tends to be polarized around studies based on primary production or on general fish-stock abundance." Furthermore, this situation has become institutionalized creating "a hiatus in the very area where most study is needed"—that is, in the gaps between marine ecology, oceanography, and fisheries. The Board summarizes, in part, as follows: "Fisheries ecology combines questions of great scientific interest with problems of significant social import . . . interests at present [are] divided by organizational barriers and funding criteria."

Given this situation, and the hypothesis I have posed, I would like to turn to a specific example, the walrus, *Odobenus rosmarus*—the "tooth-walking sea horse"—of Beringia. Marine mammals have also been subject to "yield theory" in our management of them, albeit that the theory was originally meant for fish; the "new management policy" of the International Whaling Commission is based, still, on the deterministic "maximum sustainable yield" model. Be that as it may, the walrus illus-

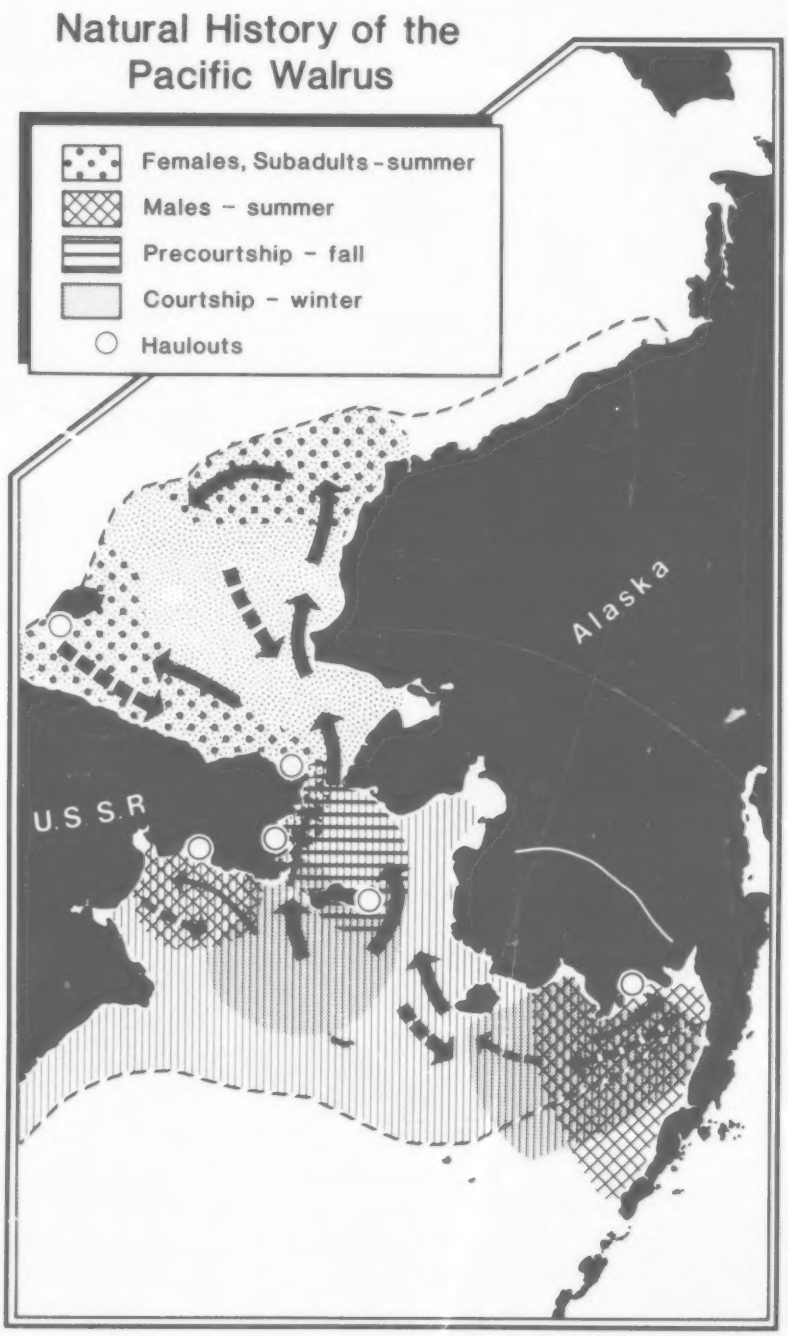

FIG. 6. Natural history of the Pacific Walrus, *Odobenus rosmarus divergens*. Note that males and females segregate during summer. Courtship occurs during winter in eastern and western segments of the Bering Sea shelf.

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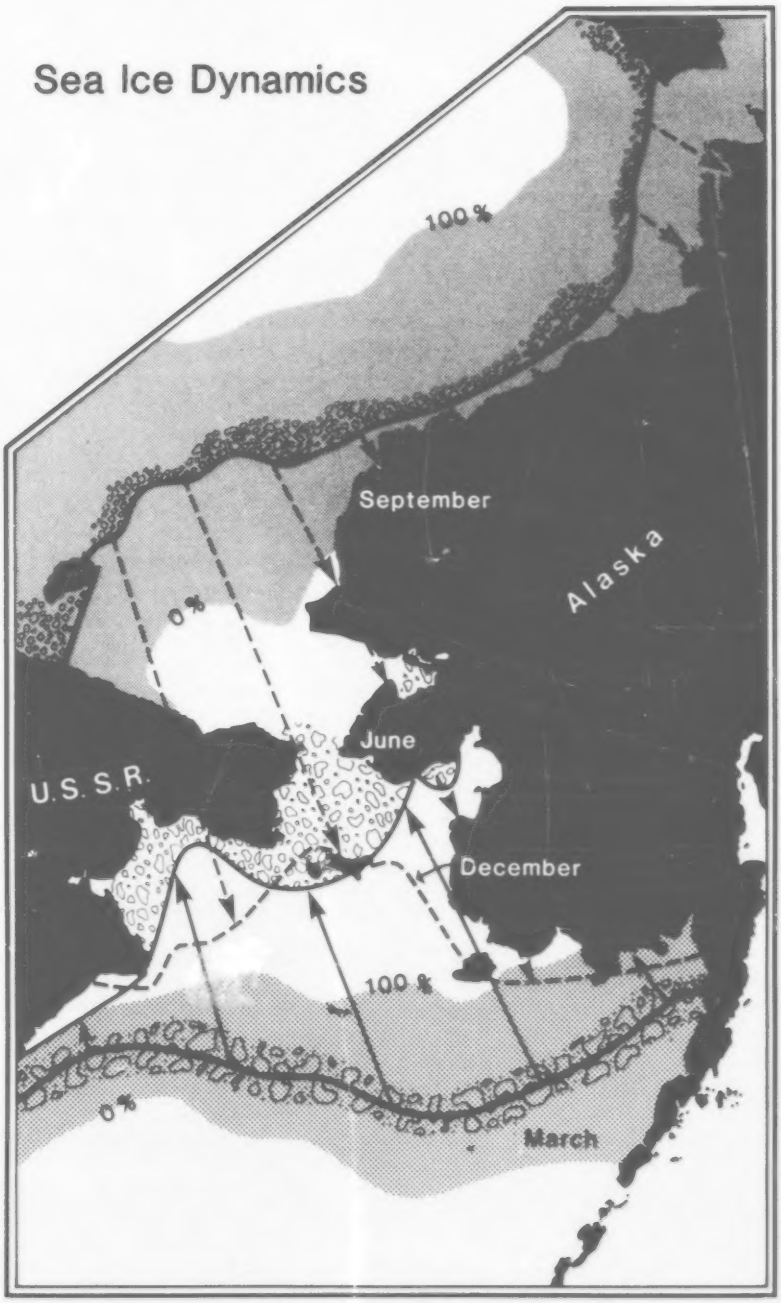

FIG. 7. Beringian sea ice dynamics, by season. The shaded areas in both summer and winter express the range of probabilities of the extents of the occurrence of the ice edge.

trates factors that must be considered in recruitment, effects on community structure and nutrient cycling, and requirements of determining "critical habitat."

Figure 6 shows the "verbs" of the walrus life-style. This generalized pattern is, of course, an assemblage of situations over several years; it is not an exact pattern for any one year, and it varies according to environmental factors. For example, sea ice dynamics are a major causal factor in walrus movements. Figure 7 illustrates the extent of sea ice movement over the course of the year and the great variation involved. Comparing sea ice movement with walrus distribution allows us to hypothesize that not only sea ice movement, but also ice structure has much to do with where the bulk of walruses may occur. Walruses may be found in winter mostly where thick, "white" ice and intersecting "leads" occur together ("broken pack"). Figure 8 is an analysis of the chance that broken pack will occur in segments of the Bering Sea during the maximum ice period of March–April. It so happens that this broken pack area is where walruses court, mate, and endure late pregnancy to early pupping; also, it is an area where heavy feeding occurs. Feeding and breeding together at one place is reason enough to call this area "critical habitat." It should be obvious that this area is defined mostly by the physical meteorological and oceanographic events that determine sea ice dynamics. It would be interesting to speculate on how such dynamic areas would be protected under Section 7 of the Endangered Species Act. (The endangered bowhead whale, *Balaena mysticetus*, also inhabits the broken pack in winter.)

Physical events are by no means all that must be considered in management. What of the biology and ecology of marine mammals in general? Can predictions be made from species to species? Figure 9 is an attempt to define the comparative "roles" of species of marine mammals (*cf.* Ray, 1981). Paramount is the fact that marine mammals range in their adaptations widely, as do other groups, but tend to varicus adaptive extremes involving combinations of reproductive strategy, food obligateness, and habitat requirements. Confining ourselves to food for the moment, we might speculate about the effects of their prediction. Do such top predators "control" (I am aware of the bias of this term) community structure, nutrient flux, and productivity? Ecological control mechanisms are widely studied in terrestrial, fresh water, and nearshore systems, but are peculiarly absent from studies of commercial fishes and marine mammals. The inescapable impression, from perusing the marine literature, is that "bottom-up" ecology prevails—that physical processes and primary or secondary productivity are supposedly to determine the fates of species higher in the trophic structure. But is this compatible with an ecosystem viewpoint?

There are alternatives. One is to ask to what extent "top-down" effects on community structure and nutrient cycling control whole ecosystem processes. Polar seas are characterized by low species diversity, but very high biomasses of a few dominants. The walrus demands high energy input; it consumes bivalves heavily and has increased markedly in numbers recently (Fay, 1982), with probable effects on the abundance and population structure of prey organisms, as well as on overall community structure. Has community metabolism also been changed? It seems reasonable to me to answer: probably so, with the result of altered demand for nutrients, both quantitatively and qualitatively, and altered routes for cycling as well.

The ultimate question concerns the magnitude of this effect. Walsh (1983) has provocatively summarized nutrient processes in shelf systems, including the carbon budget for the Bering Sea. No analysis is included for large organisms. This poses problems in face of the enormity of their feeding and their physical effects. The gray whale, *Eschrichtius robustus*, is estimated by Johnson and Nelson (1984) annually to perturb over 22,000 square kilometers of benthic sediment in its feeding in the northeastern Bering Sea alone; others of us (*cf.* Ray, 1984) estimate that walruses perturb about 75,000 square kilometers in the area of broken pack each winter. And these are only two of the many creatures,

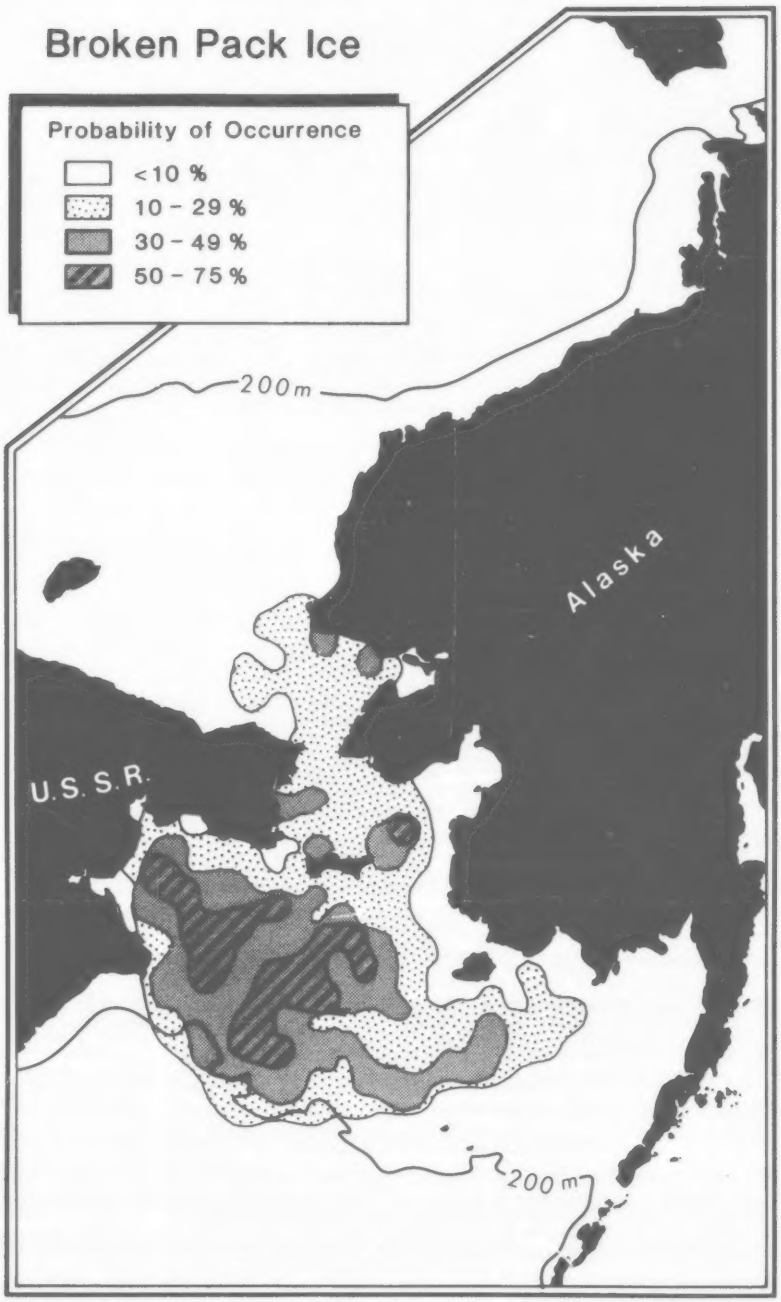

FIG. 8. The probability of occurrence of broken pack that is the favored walrus habitat in winter. Analysis is over a ten-year period from 1972 to 1982. The darkest shading indicates highest occurrence of broken pack.

big and small, that feed on the bottom there. Do these examples indicate "control"? If one takes an ecosystem view, then one is forced toward the affirmative.

Returning to the problems of fisheries, on what basis must management be placed? Is it not a most urgent issue of our times that ecosystem viewpoints ascend to primacy in both science and managment? Reichle *et al.* (1975) characterize ecosystems as possessing features of persistence and growth, maximum persistent biomass, homeostatic feedbacks, an energy base, element cycling, and regulation of rates: "A system . . . persists through time due to the interaction of its components . . . ecosystems are energy-processing units regulated by, and intrinsically connected to, the cycle of nutrient elements in the system." This being the case, there is simply no way to ignore the ecology of large organisms if we are to comprehend the science of the sea or learn to predict fisheries.

Just to point out one more complexity, Walsh (1983) concludes that not all shelf primary productivity is grazed. As odd as this seems, there are good data for it. However, this seems even odder in view of the apparent fact that primary productivity cannot account for the high energetic demands of all the fishes, birds, and mammals that occur over many shelf areas. Where does their support come from? I do not believe that this question can, at present, be answered. A recent symposium (Falkowski, 1980) arrived at the conclusion that oceanic primary productivity has been seriously underestimated, perhaps by an order of magnitude! This has to do with methods of sampling and that grazing rates are not well understood. Furthermore, phytoplankton organisms may act more like microbes than like higher plants, exhibiting "overflow metabolism" rather than "steady state" and in having their growth dependent on small-scale, high-frequency processes. How this relates to organisms higher up the food chain is anyone's guess.

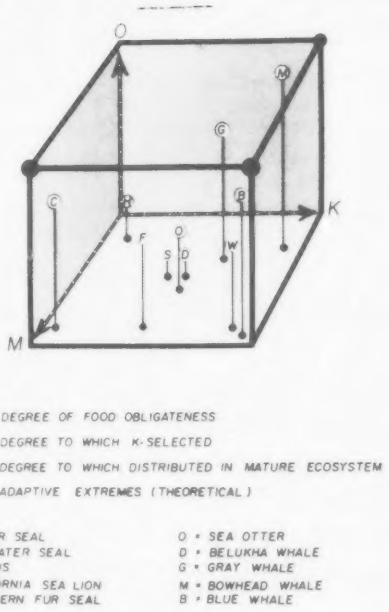

FIG. 9. Model for the comparative roles of selected species of marine mammals. Comparison among three vectors describes "ecological space" relationships in a heuristic manner.

PERSPECTIVES

Observations, derivative hypotheses, and case studies are useful to the extent that they lead to problem-solving—whether this be scientific or social. However, it is very clear that problems in human ecology require the evolution of new tools and new perspectives. For example, the global sea requires a global view, causing one to wonder whether to go down to the sea in ships is sufficient. For decades, marine scientists have struggled to comprehend an ocean that they could only sample from its surface and from place to place and time to time. The very size of the world ocean places ships at the severe disadvantage of being incapable of gathering more than point-by-point ("station" in the jargon of oceanography) data. Short-term events are extremely difficult to detect by this means. Synoptic views are not possible at all.

A part of the Marine Revolution is that, at last, satellites are capable of gathering diverse data on sea surface winds, ocean wave heights, sea surface topography, temperature, ocean color, sea ice, and other features. Working with ships for "ground truth" and in a synergistic manner, sub-

surface characteristics can be interpolated. As a result, our understanding of the sea is being altered—drastically in some cases—and the future holds promise that certain aspects of fisheries and pollution may be monitored in near real time, rather than after the fact. But lest this promise seem too great, we must be reminded that most of the required satellites are experimental and not operational. Further, current lack of a sense of political urgency and resolve appears to be a formidable obstacle to realization of scientific dreams, however "practical" and "economic" they may be.

A paper of this sort forbids publication of color imagery that would illustrate examples of this technological revolution. The Joint Oceanographic Institutions (1984), in collaboration with the National Aeronautics and Space Administration, present samples of imagery, including phytoplankton and temperature patterns for the northwest Atlantic, relationships between tuna catch and ocean color, global sea surface topography and temperature, Arctic sea ice concentration, and ocean warming during the 1982–1983 El Niño. Such data would be impossible to gather without satellites. Their data-collecting power is expressed by JOI (1984) from one short-lived satellite's example: "During the entire 100-day mission, this Seasat instrument made as many individual measurements of wind speed and direction as were collected during the previous century of shipborne observations . . . . New technology that provides global views of the oceans using satellite-borne instruments, coupled with new high-speed computers, promise major breakthroughs in our description and understanding of the ocean."

Such breakthroughs could come none too soon, and this leads to a second perspective—that of ocean "health." Health of the environment is called for in several pieces of legislation. But what is meant? Presumably, the absence of disease, to draw an analogy from human medicine. Disease itself is difficult to define. Some say it is a deviation from health and others that it is a process representing a response to injury or to insult—to normal homeostatic mechanisms, one might presume. The concepts are vague, but we know when we are sick. How can we know when the sea is "sick"?

Moore (1985) points out that we are overloading the earth's capacity to accommodate to human impact. Some economic analyses of waste disposal tell us that the sea is a better alternative than the land, at least for "benign" wastes, whatever those, in our imperfect judgement, turn out to be. Assumptions have arisen, largely from marine chemists and engineers, about the "assimilative capacity" of the ocean to accept wastes. Presumably, the "stress" of such disposal should not exceed the ocean's homeostatic capacity. What then is "stress"? Here we are on firmer ground. After Selye (1956) proposed his famous syndrome many definitions appeared, some even in ecology. Bayne (1976) defines stress as a "measurable alteration of a physiological (or behavioral, biochemical, or cytological) steady state, which is induced by an environmental change and which renders the individual (or the population or community) more vulnerable to further environmental change." The literature is replete with *measurable* changes that occur in individuals, populations, communities, and ecosystems when these are subject to various impacts, natural or foreign. That these are forms of "stress" seems reasonable.

Stebbing (1981) provides a most useful analysis of stress, which he considers as a "load," since "work is required of the control mechanisms in order to counteract any disturbances." He interprets health both as "load tolerance" and as "the capacity of a controlled process to resist the effects of load or stress." Assessing the effects of load is difficult since symptoms do not show up until there is an overload, a "last straw effect." Stebbing concludes that "no effect level" is a dubious concept; better would be an attempt to observe the operation of homeostatic control mechanisms by which equilibrium is achieved, rather than the equilibrium state itself.

Levy (1983), considering the effects of oil exploitation on arctic birds, tells us something similar: "Stress is the result of all the physical, chemical, emotional, and

other factors that cause physiological or mental tension . . . ." (This causes one to wonder about the emotional state of a fish.) Various stresses may be additive, subtractive, synergistic, or antagonistic. It is, therefore, difficult—or impossible—to predict the effect of one more stressor. "It must be appreciated that, if the balance should be tipped by these additional forces, it will be possible to attribute the disruption [of arctic sea birds] to oil only if the changes in populations are sudden and of catastrophic proportions."

Where does this put assumptions of "assimilative capacity"? Goldberg (1982) likens assimilative capacity to "a titration that chemists are accustomed to carrying out in their laboratories . . . in which pollutant materials are added to a given body of water and an end point is sought, which is determined by the amount of pollutants that the waters can handle without an undesirable effect or an unacceptable effect, *i.e.*, the loss of a marine resource." One could accuse this statement of ecological naiveté, but actually it addresses several matters that I have attempted to put into Figure 10. Assuming that each stress has some effect (reasonable by Stebbing's model), there are several levels from T1 . . . T5 that we can identify. These levels have to do with our ability to *detect* effect; generally, our abilities grow logarithmically with time in this respect. They also have to do with the amount of *effort and money* that society is willing to put into both research and monitoring. Finally, they have to do with a *social decision*; what constitutes "undesirable" or "unacceptable" is not only a scientific matter.

The opportunity is that "health" may be addressed through research in stress ecology. Unfortunately, toxicology and marine chemistry, wherein most pollution studies rest, have not been traditionally been rich in natural history and ecology, although there exist efforts to counteract this through the new science of "ecotoxicology" (see particularly Levin and Kimball, 1984). Former toxicological assumptions that for every pollutant there is a level that produces no effect, and the overwhelming tendency of pollutants in the ocean to be considered one by one, as if each were placed in a separate bucket, present major challenges for future marine ecology.

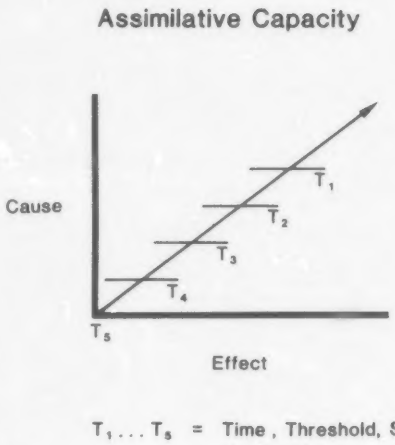

FIG. 10. Model for "assimilative capacity" of the sea for pollutants. Three interpretations of T1 . . . T5 are possible: (1) improving methods for detection of impact with time, (2) a threshold (ecological or biological), and (3) the degree to which society is willing to tolerate the effect.

CONCLUSIONS

> The sea never changes and its works, for all the talk of men, are wrapped in mystery.
>
> Joseph Conrad, *Typhoon*

The sciences of the seas today stand at a crossroads. There are two basic concerns: first, can a unified science of the seas be developed? Second, how could this aid in addressing the accelerating problems of the marine revolution—of human ecology? If we see science as a process (*cf.* Mayer, 1984), then its evolution clearly is toward unification of hypotheses and goals. If we see how social processes link with scientific concepts, then the urgency of application of our science becomes clear. However, the marine sciences are presently hardly unified. A visit to the library will demonstrate that there are about three and a half ways of studying the sea: marine biology, the oceanographies, fisheries, and the coastal zone (this is the "half," as about 50% concerns the land). Marine biology concerns

biology, physiology, and ecology of marine organisms. It is mostly an inshore science, practiced more in tidepools, reefs, and estuaries than on the open sea. The oceanographies are three: physical, concerning the lifeless sea; chemical, or the sea as a mixing bowl of reactants; and biological, dominated by the Lilliput of plankton. Fisheries takes over on the larger, biological end of things, as it relates almost exclusively to the larger marine inhabitants of commerce. A student, attempting to relate all of these disciplines, runs into formidable problems.

Can a science of "oceanology" be derived? This thought has been about for some time and there are even a few courses of study along these lines. But the tides of inertia are strong in science and academe, the economy, and government. The difficulties of relating the marine sciences to one another is perhaps best illustrated by urgent problems in fisheries ecology, considered above.

Considering reference and teaching texts, perhaps the most stimulating volumes are the collections of papers from symposia and the like, but these are comprehensible only to advanced students. The beginning marine science texts themselves are largely organized about the disciplines mentioned above. I have not yet found an "oceanology" text in the sense of truly integrating these disciplines. What is also apparent is that few texts begin with concepts or hypotheses that organize thoughts. "Fact-ridden encyclopedias" (Moore, 1985—see above) indeed describes the world of the texts and reference works of much of marine science. This is *not* to say that encyclopedic treatments are not useful and necessary—but secondarily, *after* a substantial beginning has been made. In any case, we presume too much that students are already "hooked" and will tolerate or remember all that we throw at them willy-nilly.

I have an argument, too, with general ecology texts. Their strong bias towards the third of Earth we call the land prejudices, and sometimes wrongly interprets, marine phenomena in the mind of the user. The sea part of the planet is usually confined to a small section by itself, the presumption being that the principles that have gone before apply generally to the very different terrestrial and aquatic systems. In our terrestrially oriented way of thinking, we hear of the deserts, forests, tundra, grasslands, and the seas. How would it strike you to hear of the benthos, pelagic waters, reefs, sea grasses, and the land? We clearly need both unification and separation in the presentation of ecology.

Moore (1985) puts it this way: "Science is an intellectual enterprise with a beauty, importance, and relevance that make it one of the most notable achievements of mind and civilization." The wisdom and urgency of that statement can hardly be overestimated. The Marine Revolution is in many ways a "last resort." The *knowing* that science can provide and the *doing* that it can assist may well be critical for the maintenance of civilization as we know it. Many of us who study the sea and its creatures share the sense of mystique that much of society also feels. Perhaps the finality of "conquering" the last of Earth's horizons will force the Humane Revolution of which Moore speaks. In any case, there will be no substitute for presentation of unified, ecosystem-based concepts to students and the public, devoid of terrestrial prejudice; that is, we must learn to see the sea and its organisms and processes as they are, in their own right.

As man is still the hunter-gatherer by sea, the primacy of *knowing* the sea is even more fundamental than for the land. Our fisheries depend on *natural processes*, as we have not yet learned to domesticate the seas to our liking. Where do the concepts lie that will challenge the students who will make future decisions? How can we learn to manage natural processes that are quite beyond our capacity to domesticate? Such is the state of our knowledge and technology that attempts to "control" or "engineer" the sea can lead only to catastrophe or to "lucking it out" unpredictably.

Man the "hunter-gatherer" is a put-down to a growth-oriented, technologically infatuated society. It puts us in the position of Stone Age dependency, having to understand how to make do with what nature

provides. But is that not rather an opportunity-laden self-recognition? Why are simplistic ideas about "assimilative capacity" so attractive? Probably because the majority of politicians and of society—and of scientists too—do not think ecologically. The obvious solution, in the long term, is to teach to perceive critical relationships and essential processes, including the process of science. Science is, in fact, a no-lose situation; hypotheses, if intelligently posed, whether proven right or wrong, must instruct.

Elizabeth I wrote in 1580 to the Spanish Ambassador:

> The use of the sea and air is common to all; neither can a title to the ocean belong to any people or private persons, forasmuch as neither nature nor public use and costom permit any possession thereof.

A scant three centuries later, from the age of Shakespeare to whatever may endure of our times, the seas are becoming possessions of nations; during the 1600s three miles, now to two hundred. What next? And, which system is best, a commons or ownership? Can science tell us the answer? Holdgate (1978) observes that "The ecologist has been too prone to behave as a latter-day prophet, seated remotely in his laboratory and functioning in a fashion reminiscent of the Delphic oracle." Holling, in the same volume, reminds us that good scientific studies do not necessarily lead to better decision-making, nor does systems analysis allow us to choose the best alternative among several plans or programs. Decisions are made on at least three levels (*cf.* Andrews and Waits, 1978): social norms, individual preferences, and ecological functions. Nevertheless, there is little doubt in my mind that good decisions cannot be made *without* good science. The obvious task for scientists is to lead the way in that regard, both in research and, perhaps more importantly, in teaching.

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Human Ecology: The Subversive, Conservative Science[1]

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SYNOPSIS. Paul Sears identified ecology as a subversive science; William Ophuls, referring primarily to its human applications, called it a conservative science. Both characterizations are correct. Human ecologists aim to conserve natural resources, thereby making it possible for our posterity to enjoy a quality of life at least equal to ours. Frequently this kind of conservatism is at odds with the conservation of traditional religious beliefs, political practices, and social privileges: hence the aptness of the adjective "subversive." The essence of human ecology is found in a few propositions of the sort that mathematician E. T. Whittaker called "postulates of impotence." These lead to simple but profound generalizations, of which a dozen are offered here.

Identifying a single science as both "subversive" and "conservative" may seem a perverse thing to do, but I will explain the combination before I am through. To begin with let us see how the first adjective came to be applied to ecology. Paul Sears (1964), just two years after the publication of Rachel Carson's *Silent Spring*, asked:

> Is ecology a phase of science of limited interest and utility? Or, if taken seriously as an instrument for the long-run welfare of mankind, would it endanger the assumptions and practices accepted by modern societies, whatever their doctrinal commitments?

In the discussion that followed Sears made it quite clear that he regarded ecology as being of almost unlimited interest and utility for everyday life, acknowledging that its principles threatened many assumptions and practices in the existing social order. Sears, far from a radical in ordinary political matters, was forced to conclude that ecology is a subversive science.

A short time later Paul Shepard and Dan McKinley (1969) borrowed Sears' words for the title of a useful anthology. Before a decade had passed, William Ophuls (1973), in a remarkable dissertation offered in support of a Ph.D. degree in political science, identified the subversive threat more clearly:

> Human ecology is against the conquest of nature; against growth as we think of it; against the isolation of thought and action; against individualism as an ideology; and against moral absolutes like the inalienable rights of man. "The subversive science" is thus a pitifully weak soubriquet for ecology, which demands only that our current political, social, economic, and moral order be stood on its head.

When the human ecologist fully understands the irony of Ophuls' concluding words he realizes how lonely is the path he must walk as he is belabored by both Left and Right of the political spectrum. I would not have the ecologist turn aside because of a justifiable fear of vested powers; rather would I urge that he make use of the resources of humor, stiffening his backbone by recalling a comment made by the professional humorist Art Hoppe (1970), who caused an imaginary happy-go-lucky student radical to say: "The great thing about ecology as a cause is that everybody's guilty."

Yet another burden falls on human ecologists: the science is inescapably interdisciplinary. To quote once more from Sears (1971): "It may clear matters somewhat to modify the usual definition of ecology as the science of interrelation between life and environment. Actually, it is a way of approaching this vast field of experience by drawing upon the best information available *from whatever source it may come.*" (Italics added)

Should we, then, assemble teams of scholars to carry out the needed interdisciplinary work? The proposal seems logical enough, but this approach seldom has a

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happy outcome. Great though the personal risks may be, it is the individual who must carry out the work of synthesis. Individuals must be prepared to make mistakes and be castigated by narrow specialists. Every statement made by a daring synthesizer will tread on someone's toes. Controversy is unavoidable. Obviously a field like human ecology is not everyone's cup of tea. I happen to enjoy it. Let me see if I can explain its attractions and the way in which I think human ecology should be presented to students.

The boundless multiplication of recorded facts makes it advisable that every well-developed subject be first presented by way of broad generalizations. Generalizations are always dangerous, but they are less dangerous than a refusal to make generalizations. At the very least a generalization has heuristic value, that is, it has the potential of leading to fresh discoveries. If a statement has exceptions these are more likely to be discovered if the principle is expressed in simple, dogmatic terms. (Is this a consequence of the contrariness of human nature? Whatever the explanation, the fact is useful.)

I advance the following thesis: the heart of human ecology can be presented as a set of rather dogmatic generalizations, most of which are in the form of negative statements. Let me take as my first example a well accepted dogma from the subdivision of ecology known as "economics." (Card-carrying economists may not like to hear their specialty identified as a subdivision, but I call your attention to the fact that the names of both sciences are derived from the Greek *oikos*, house or home. Economists tend to focus only on the people in Household Earth, thus making their subject only a fraction of the total science of ecology, which deals with all of earth's inhabitants and their environment.)

Popularly expressed, the central dogma of economics is this: "There's no such thing as a free lunch." Asked if this is always true the economist replies, "You'd better believe it!" He can't prove there are no exceptions, but neither does he believe that an understandable, reliable science of economics can be created without this generalization (whether explicitly expressed or not). This dogma, which natural scientists would call a conservation principle, leads to the assumption of business practice that accounts must balance. It is intolerable to suppose, or hope, that actual income might exceed the sum of intake minus outgo. (When a set of books seems to indicate that such a miracle has occurred the cause is sarcastically referred to as "creative bookkeeping.")

Why should a major dogma be best presented in a negative form? We could have expressed the major assumption of economics in a positive way: "Every lunch has its price." I doubt very much if many people would make the idea part of themselves if the positive form had been used. There is something about a negative formulation that captures the human attention. Perhaps this fact is related to the observation of Sigmund Freud (1925) that, at the subconscious level, the human mind cannot deal with negation. Since the subconscious mind cannot deal with negation, even to refute it, the conscious mind must: so the negative form captures our attention. Whether or not this speculation uncovers the truth, the fact remains: negative statements make us think.

The greatest dogmas of the natural sciences are given in negative form: they tell us what we cannot do. Take the facetious (but profoundly true) forms of the laws of thermodynamics:

You can't win.
You are sure to lose.
And you can't get out of the game.

Here is negativity in earnest—but it gets our attention. The mathematician E. T. Whittaker (1942) has called the foundation stones of science its *Postulates of Impotence*, saying that each one

> asserts the impossibility of achieving something, even though there may be an infinite number of ways of trying to achieve it. A postulate of impotence is not the direct result of an experiment, or of any finite number of experiments; it does not mention any measurement, or any numerical relation or analytical equation; it is the assertion of a conviction of the mind, that all attempts to do a certain thing, however made, are bound to fail.

This is a remarkable, perhaps even

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shocking, view of science. That science might, at the bottom, be based on *a conviction of the mind*, rather than experiments, brutally contradicts a common textbook view of science as an aggregation of empirical statements. In a sense, perhaps both contradictories are true. We will not tolerate a dogmatic statement that always contradicts empirical findings; on the other hand, in the practice of science we put a great deal of trust in a very few dogmatic statements that have proved so useful in the past that a contradictory new empirical finding will itself be doubted for a long time before we are willing to throw out a dogma that has become "a conviction of the mind." It is, for instance, difficult to imagine an empirical finding that would lead us to scrap any of the laws of thermodynamics. Without impotence principles, without conservation laws—without *closure* of the analytical system—intellectual anarchy threatens to take over.

What, then, are the central dogmas of ecology? To begin with, ecology must admit all the conservation laws of the physical sciences. Those accepted, ecologists go on to generate additional postulates of impotence. Let me lay out what I regard as the foundation stones of human ecology.

1. *We can never do merely one thing.* Implicit in Darwin's *Origin of Species* is the image of a complex web of life, with every species having strong or weak ties with every other species. Darwin was not the first person to be aware of widespread connections in the world. In the words of Ophuls (1977): "With their vision of total interdependence and connectedness the mystics were in effect the first ecologists." To John Muir is attributed the saying that "Everything is connected with everything else." These are less the words of a scientist than of a mystic, though they are often identified as the "First Law of Ecology."

Muir's mystical sentence is criticizable on two grounds. First, it is a positive statement and so is not well suited to be a prime principle. Second, by dispersing our attention over literally everything, it interferes with our seeing particular things. To achieve practical control of natural forces we need to focus on singularities, even though we thereby risk not seeing the forest for the trees. Pursuing the opposite course puts us in danger of becoming the mystical Hamlets our opponents accuse us of being.

In contrast to Muir's statement, the assertion that "We can never do merely one thing" (Hardin, 1963), though it does not tell us exactly what to look for, does tell us to look very hard at every proposed intervention in an existing system to make sure we are not about to carry out actions we may later regret. Muir's statement encourages passivity and fatalism; the revised version encourages study and prudent action.

2. *No effects are truly "side effects."* Strictly speaking, all effects are effects, *period.* He who wishes to control the perceptions, and hence the actions of others, labels as "side effects" those consequences he does not wish people to become aware of or to act upon. A variant of this rhetorical ploy is pinning the label "external costs" or "externalities" on the costs a businessman *wants to keep external* to the account books of his company (Hardin, 1972).

3. *No system can long survive the effects of unopposed positive feedback.* This, of course, is the heart of the Malthusian insight, an insight that has been vigorously attacked by many in the academic community—particularly by sociologists—for more than a century. I know of no better way to sweep away the mental miasma of the dream of perpetual growth than by exposing the student to an essay by A. A. Bartlett (1978), "Forgotten fundamentals of the energy crisis," the printed version of a lecture Professor Bartlett has delivered more than seven hundred times to general audiences.

Perhaps the simplest way to bring home to the average citizen the magnitude of the threat of unopposed positive feedback is to point out the logical consequences of putting out money at interest. Suppose that the thirty pieces of silver Judas received for betraying Christ had been worth $30; and suppose that he had put this into a bank account bearing 5 percent compound interest, payable in gold. Presuming the present price of gold, the initial capital would amount to about 2.5 grams of gold. How long would it take for the Judas

Account to be worth a weight of gold equal to the weight of the entire earth (5.983×10^{27} grams)? Just 1,292 years. This means that at about the time of Dante's death the heirs of Judas could have presented themselves at the bank and demanded the world's weight in gold. Such is the power of exponential growth (or "geometric growth," as Malthus called it).

4. *Negative feedback can be a positive boon.* Banks sell their services with the implied promise of absolute safety for savings accounts—forever. So long as such accounts bear a positive rate of compound interest, no matter how small, such a promise is ridiculous. Interest is tolerable only because the exponential growth it promises is opposed by bank failures, theft, fraud, government expropriation, revolution, conquest and repudiation. We regard all these negative feedbacks with distaste, but one or more of them must be included in every workable system in a finite world, if no limit is put on time.

More relevant to our interests, the positive feedback of biological growth must be opposed by the negative feedbacks of predation, parasitism, socially induced sterility and many other factors that interfere with reproduction and favor death—in Malthus' terms, by "misery and vice." Biologists are in a particularly favorable position to oppose the Pollyanna attitude that has been nurtured by the remarkable technological progress of the past two hundred years. Death is still a necessity and a boon.

5. *"Thou shalt not transgress the carrying capacity."* If ever agreement is reached on a Decalogue of Ecology, this surely will be one of the commandments. If the language seems too theological, reword the advice to your taste, but do not lose the imperative flavor. To disarm the defences of Growthmanship, it may be well to bring forward the implications of carrying capacity by first analysing a non-human situation, say the history of the reindeer herd on St. Matthew's Island (Klein, 1968; Hardin, 1982). Two evils follow from transgression. First, per capita well-being falls as overpopulation takes over. (This phenomenon, in fact, gives us an operational definition of the controversial word "overpopulation.") Second, once transgression has occurred, the carrying capacity in successive years spirals downward to very low levels. Uncorrected transgression can ultimately extinguish a population.

6. *The "sanctity of life" must give way before the "sanctity of the carrying capacity."* This statement presumes that "sanctity" is an admissible concept in rational thought, and that a cardinal aim of policy is to minimize the loss of life (over an extended period of time). In discussing problems of game management biologists should be able to convince students that maximizing the number of healthy lives is the proper aim of game management. The herd on an overcrowded range is peremptorily thinned, by killing if necessary, so as to reduce the size of the herd to the carrying capacity; and it is kept at or below that level so as to maximize the amount of life over a long period of time. *This* year is only a moment in time, and the present population is only a fraction of the total. The rational game manager kills in order to maximize the number of lives over time. It is carrying capacity, not the individual life, that needs to be invested with "sanctity" (Hardin, 1976). This should be obvious, but the teacher who discusses game management problems will discover that some students bridle at the thought of killing an animal today even if this is the only way to save more animal lives tomorrow.

Application of the principles acquired in game management to human situations will be strongly resisted. In controversial areas it is not the function of the teacher to demand agreement; his role is to expose assumptions and arguments. It may come as a surprise to biologists to learn that some professional philosophers (for instance, Taurek, 1977) have ranked "fairness" above life itself in discussing human analogs of the game management problem. Triage aimed at maximizing the number of lives saved (Hardin, 1980) is viewed by Taurek as "unfair," and he would rather be fair than save lives.

One cannot but wonder how such a philosopher would react if he were *in fact* made responsible for the well-being of a herd of

animals in an overpopulated range. Out of "fairness," would he passively allow almost an entire herd to die of starvation, as the reindeer on St. Matthew's Island did, rather than "unfairly" eliminate a considerable number so that the environment could be saved for the reindeers' posterity?

I find it difficult to believe that our philosopher would stick to the principles he evolved in the quiet of his study. (I find it even more difficult to believe that anyone would knowingly hire such a philosopher for the management of herds on an estate he hopes to pass on to his posterity.) I have made numerous public recommendations for dealing with the problems of regional hunger now surfacing with increasing frequency throughout the human world (Hardin, 1974, 1976, 1980, 1982, 1985). For more than a decade ecologists have pointed out that the population of Ethiopia is beyond the prudent carrying capacity of the land. Now that the crash has come well-intentioned people, upholding the sanctity of life rather than the sanctity of the carrying capacity, are eagerly sending in food from the outside thus ensuring that the Ethiopian population will remain above the carrying capacity. The consequences of good intentions that are uninformed by ecological principles will be the transformation of a presumed temporary crisis into a veritable permanent crunch (Hardin, 1974).

It is time to recall the prescient words of William Ophuls (1973): "Human ecology is against . . . the isolation of thought and action; against individualism as an ideology; and against moral absolutes like the inalienable rights of man." Ophuls' insight may be too strong a medicine for the student to take; the good teacher, like the good psychoanalyst, must carefully choose the time for reevaluation.

7. *Not all elements of the human carrying capacity are expansible.* We are rightfully proud of the technological advances humanity has made in the past two centuries. These advances have significantly enlarged the usable carrying capacity of the earth, but only with respect to *some* of the elements that we include in the aggregative term, "carrying capacity."

To the extent that capital investment is an important element of production costs, population growth brings the benefits of economies of scale. Food production and energy extraction have increased greatly, but the fundamental absorptive capacity of the earth for harmful waste products has not increased. Time moves no faster now than it did a thousand years ago, so high quality goods that require much time in their production, *e.g.*, cabinet-quality hardwoods, have become increasingly scarce. Amenities that cannot possibly be increased in quantity—lonely beaches and wilderness are examples in point—continually decrease on a per capita basis.

8. *Population growth ultimately makes democracy impossible.* Easy communication is the *sine qua non* for an enduring democracy. All communication functions are inherently afflicted with *dis*economies of scale, since (for every well defined communication network) the burden created by the communication of n people increases as the *square of n.* This burden expresses itself in information-overload, which leads to misunderstandings, social pathologies, and (ultimately) the acceptance of a totalitarian regime as the least of the evils available to an overpopulated political unit. In the face of unlimited population growth the *word* "democracy" can be retained, *but not the fact.*

Biology teachers usually avoid dealing with political matters, but I recommend that in this case they depart from custom to emphasize this scale effect. Ever since Malthus, apologists for perpetual population growth have shown great ingenuity in the selection of data to bolster their position. (For recent instances see Simon, 1981, and Simon and Kahn, 1984.) Always implicit, and often explicit, is their repugnance at the thought of the loss of individual freedom through population control measures. It needs to be brought home to the Growthmanship crowd that the fundamental diseconomies of scale inherent in communication mean that the freedom they cherish cannot be retained if the growth they advocate comes to pass.

When Pasteur and others brought about a revolution in public health they intended

only to conquer disease. We, the beneficiaries of this great revolution, now face the bitter truth that "We can never do merely one thing." Now that the providential negative feedback of density-dependent crowd-diseases has been eliminated, the question that people in all societies must ask is this: In which way would you prefer to lose your freedom? Through the community's regulation of the number of children, or through Nature's cruel elimination of the excess population?

9. *Selection dictates the direction of evolution.* This is so obvious to biologists that the point need not be debated. Let us go on to see some of the practical applications of the principle.

10. *Every biocide selects for its own failure.* Until *Silent Spring*, technological optimists seldom had to face this principle. When first introduced, DDT did indeed seem a miracle stuff; but it selected for insects that had genetic resistance to its action. Similarly, antibiotics select for microbes that are genetically resistant to their toxic qualities. Control of pests and disease germs is not impossible, but neither is it simple. No single control agent can be expected to be effective for very long; combinations and alternations must be used. The price of liberty, it has been said, is eternal vigilance; this is also the price of freedom from disease.

11. *Every human law selects for its own evasion.* Discussion of pesticides sets the stage for discussion of phenomena of human ecology customarily relegated to political science. I recommend that such matters be brought into a course in human ecology, not as an act of academic piracy, but to emphasize the artificiality of academic boundaries and the unity of knowledge. Obviously the word "selects" is here used in a sense different from the biological meaning. Genetic selection is not involved; the selection invoked is of the most general sort. Behavior is socially selected for and rewarded; and as bystanders observe the way an unintended reward system works they may be tempted to imitate the rewarded behavior. A few examples should clarify the idea of social selection.

Every new tax law creates new "loopholes": people who discover them are rewarded with lower taxes. An unmanaged commons (Hardin and Baden, 1977) selects for the selfish behavior that will, under conditions of scarcity, tragically exhaust the resource (Hardin, 1968). A managed commons, usually called "socialism," selects for managerial behavior that primarily protects the interests of the manager. This gives rise to the ancient question, *Quis custodiet ipsos custodes?*—"Who will watch over the watchers themselves?" On the other hand a privatistic politico-economic system favors a positive feedback of social power that threatens to create unbearable economic and social inequalities (Hardin, 1963).

12. *No inning is the last inning.* There is no easy answer to the problem of creating an acceptable and stable social order. In biology, the "climax community" is recognized as a fiction fostered by the short time span of human attention. In principle, every species is part of the selective environment for every other species, so change in the numbers of one species tends to set off a prolonged domino process of selection and change in other species. In human sociology, analogous processes (even in the absence of genetic differences and genetic changes) lead to similar domino-processes.

The environmentalist who focuses on strictly scientific facts is likely to become disillusioned as he observes the multitude of ways in which people can evade sensible environmental laws and regulations. In the biological realm, selection determines evolution; in the social realm, rewards (intended or not) determine behavior. A strict law governing water quality may be evaded by shifting pollutants to the atmosphere. Control the air as well, and polluters may bury their by-products in the ground. As for the regulators themselves, in their desire to survive and prosper they may find it to their personal advantage to be "captured" by the powers they are supposed to regulate. Once captured, they are in a good position to be offered much higher paying jobs in the regulated industries.

In human affairs there is no such thing as a last inning, and the ways in which com-

peting forces can more or less adjust to one another are beyond numbering. The complexity of a politico-economic system is comparable to the complexity of the ecological systems biologists study. Put the two together into a system of systems and we have *real* complexity. The most carefully thought out intervention in this system of systems will not always produce the results we want. Interventions are often counterproductive.

Having begun with Sears' perception that ecology is a subversive science, let us end with a balancing contention by Ophuls: "Ecology is a profoundly conservative doctrine in its social implications" (Pirages, 1977). The truth of the statement depends on the meaning imputed to the word "conservative."

In a century and a half the word has accumulated many meanings, some of them contradictory. No definition can be said to be *the* correct one. Whenever we hear the word "conservative" we should automatically ask, *conservative of what?* Which of the many known kinds of conserving actions can the human ecologist, *qua* ecologist, support?

Conservative of ancient beliefs? Science is ineluctably married to doubt, and the antiquity of a belief is no warrant of its truth—though it may be a reason for seriously examining it. Many non-scientists would, if they could, enforce public belief in unexamined ancient dogmas for the sake of social stability. As a scientist, no ecologist can support such an action. In this sense, ecology is clearly not conservative.

Conservative of existing political and social institutions? Conditioned by his First Law, "We can never do merely one thing," the ecologist has to be somewhat sympathetic with this policy. This hesitancy to embrace institutional change is, for the ecologist, less a matter of principle than a matter of prudence. The undeniable bad effects of institutional arrangements that worked well under conditions of lower population densities makes the ecologist more willing than non-scientific conservatives to seek improvements in human institutions.

Conservative of existing social privileges? An ecologist sees no compelling reason for supporting the existing power structure. Because of the positive feedback of social power those who possess it will do quite well enough supporting their own interests. In fact, in the absence of deliberately engineered negative feedbacks in the social realm, the powerful will do too well. The eternal need for limitations on the runaway feedback of social power is a point that escapes the understanding of doctrinaire "libertarians."

Conservative of environmental resources and amenities? Yes: this is a primary interest of human ecologists, who wish to preserve as much as possible of our real wealth for subsequent generations. With some political and economic conservatives human ecologists can make common cause. On the other hand there are many people who now call themselves "conservatives" who have absolutely no interest in this sort of conservation. To this type of conservative the proposals of human ecologists seem subversive. In turn, ecologists say that those who refuse to regard themselves as posterity's trustees of nature's riches do not deserve the name "conservative." In the game of survival, the conservation of any particular social system is ultimately futile in the absence of the truly essential conservation of natural resources.

The greatest commonality between ecological conservatives and political conservatives is in their attitudes. Two common attitudes deserve notice. First, committed conservatives of all kinds hold that the social value of actions is determined more by their consequences than by the intentions of those who performed them. "The road to Hell is paved with good intentions." Good intentions, though they may explain poor results, do not excuse them.

Secondly, true conservatives take a long view of time. Not as long as the geologists, whose unit may be a million years, but certainly much longer than that used in business-as-usual and politics-as-usual, where the horizon is no more than five years off. Such short-sightedness grows logically out of the economic practice of "discounting the future" in terms of the going rate of interest (Hardin, 1975). The higher the rate of interest, the more heavily the future

is discounted, which means that shortsightedness "pays." Times of trouble—inflation, social disorder, revolution—raise the interest rate and thus make provision for the future more difficult. In consequence, it becomes ever harder to escape the trouble. Positive feedback generates a vicious circle.

The economic theory of discounting the future makes a certain amount of sense, but the permanent features of an enduring civilization are built on actions that ignore this sort of economic theory. There are times in the life of every community when even the investment that must be made in bearing and rearing children cannot be justified by "hard-nosed" economics. It would be going too far to claim that the future belongs to those who reject the economic theory of discounting; but the future does belong to the *descendants* of those who reject the simple implications of this theory. Such rejectors are the true conservators of civilization. Subversive ecologists can take pride in the fact that they are true conservatives.

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Films and Videotapes in Human Ecology[1]

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As part of an effort to make faculty aware of the importance and availability of audiovisual resources for the teaching of first-year courses in biology at colleges and universities, the Education Committee of the American Society of Zoologists is sponsoring film programs to augment the "Science as a Way of Knowing" symposia presented at the ASZ annual meetings. Subsequent to the first "Science as a Way of Knowing" symposium held in Philadelphia (1983), a discussion of films and videotapes available to supplement the teaching of evolutionary biology was published in the *American Zoologist* (Hart, 1984). The rationale for using audiovisual materials in teaching, strategies useful in the search for relevant films and videotapes (any discipline), specific sources of information for obtaining appropriate films and titles of materials pertaining to evolutionary biology were presented. The "Science as a Way of Knowing" symposium held in Denver (1984) focused on human ecology and two film sessions were organized by us as part of the program. The present article deals with several of our experiences in locating audiovisual materials in this discipline and lists the titles of a number of films and videotapes that one might find useful in the classroom.

We have interpreted human ecology as being concerned with the interrelationships between mankind and environmental resources. When we began our search for relevant film titles, it became apparent that human ecology films and videotapes do not always appear within the "Science" section of catalogues; indeed, many excellent offerings are listed under "Social Science." Also, it is important to narrow one's search as we were unable to find any such "Human Ecology" heading in the resource materials that we consulted. Film and videotape titles appear under such headings as: Conservation, Ecology, Energy, Food Issues, Natural Resources, Overpopulation, Pollution, etc. Our examination of the listings under such headings suggests that there are many outstanding films and videotapes for classroom instruction. The titles and descriptions of these films and videotapes may be obtained from a variety of sources. For example, most of the films and videotapes listed by title below are readily available for rental from major university film libraries (*i.e.*, University of California, University of Missouri–Columbia, University of Iowa, University of Illinois, Indiana University, University of Michigan, Pennsylvania State University, and others). Additional sources of information include *NICEM* (University of Southern California, University Park, Los Angeles, California 90007), *The Video Source Book* (National Video Clearinghouse, Inc., 100 Lafayette Drive, Syosett, New York 11791) and the computer search services described by Hart (1984). Generally, the Audiovisual or Media Resources Centers of colleges and universities have a number of catalogues and supplemental information that are useful in locating appropriate films and videotapes.

We provide below a list of several 16 mm films and videotapes which, based on title and description from numerous film cata-

[1] From the Symposium on *Science as a Way of Knowing—Human Ecology* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1984, at Denver, Colorado.

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logues, would appear applicable to teaching various aspects of human ecology. This list is by no means all-inclusive; it is comprised primarily of audiovisual materials published in the last decade and directed at college and university level audiences. We have not had the opportunity to preview most of these films and videotapes. Hence, the quality of films may be variable and some older films may not be suitable for some applications. You are urged to find out as much as you can about a film or videotape before making your selection for the classroom. Although we have attempted to categorize the films and videotapes by topic, it should be pointed out that our selection is clearly subjective. Finally, we would be delighted to learn of additional audiovisual materials for past (evolutionary biology) and future (genetics, developmental biology) "Science as a Way of Knowing" symposia.

POLLUTION

Acid Rain: Requiem or Recovery
Ah, Man—See What You've Done
Air
Air Is for Breathing
Air Pollution: Sweetening the Air
Alone in the Midst of the Land
And on the Eighth Day
Ark
The Atmosphere in Motion
The Cities: A City is to Live In
Complex Human Ecosystems
Danger! Radioactive Waste: Parts 1 and 2
Death Be Not Loud
Dioxin
Don't Hold Your Breath
Energy Consequences
Eternal Water
The First Pollution
The Second Pollution
The Third Pollution
Hazardous Waste Options
Hazardous Waste: Who Bears the Cost
Knowing It Survives Us
A Love Canal Family
Man: The Polluter
Mare Nostrum
Mud
The Myth and the Parallels: A Story of Conservation
No Deposit—No Return
Noise: The New Pollutant
Open Space
Our Poisoned World Series
A Plague on Our Children: Part 1—Dioxins
A Plague on Our Children: Part 2—PCB's
The Poisoned Air
The Poisoned Planet
Pollution is a Matter of Choice
Pollution of the Upper and Lower Atmosphere
Population and Pollution
The Quiet Crisis
Radiation: Impact on Life
Rise and Fall of DDT
Secrets of Limestone Groundwater
The Sky's the Limit
Stream
Survival
Troubled Water (Oasis in Space Series)
Urban Impact on Weather and Climate
Water
Water: A Precious Resource
Water: The Effluent Society
Weather: Who Votes for Rain?
"We Have Met the Enemy and He Is Us"
What Are We Doing to Our World (The 21st Century Series) Parts 1 and 2
What Price Progress?

THE IMPACT OF MAN ON HABITATS

The Aging of Lakes
The Arctic: Our Last Chance
At the Crossroads: The Story of America's Endangered Species
Before the Mountain Was Moved
Cry of the Marsh
Deep Threat
Ecocide: A Strategy of War
The Edge of the Bay
The Endless Sea
Environment in Crisis: The Aging of Lakes
The Everglades
From the Desert to the Sea
Habitat: A Special Place
Inside the Golden Gate
Let the Little Lake Live
Man and his Natural Environment—The Creek
The Rocky Mountains (The Nature of Things—The Last Stand Series)
The Salt Marsh: A Question of Values

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Survival on the Prairie
Tomorrow is Maybe
Our Vanishing Wilderness: Prudhoe Bay—or Bust!
Our Vanishing Wilderness: Slow Death of the Desert Water
Our Vanishing Wilderness: The Chain of Life
Water Wars: The Battle of Mono Lake
Where Did the Colorado Go?

OVERPOPULATION AND FOOD SUPPLY

The Agricultural Revolution: Man as Food Producer
And Who Shall Feed This World? Parts 1 and 2
Botanic Man #9: Extinction is Forever
Can the Earth Provide?
Can the World be Fed?
China: Feeding One-Fourth of the Human Race
The Choice is Ours
Diet for a Small Planet
Earth: No Vacancy—Limits to Growth
The Earth and Mankind Series (Six 28 min b/w films produced by the National Film Board of Canada)
Ecology: The Silent Bomb
The Edge of Survival
Food and People: An Introduction to the World's Food Problems
Food for a Modern World
Food: Green Grow the Profits
Food Revolution
Food Supply: Its Effect on Civilization
A Future for Every Child
Grain of Conscience
Growing Concerns
Hunger
Hunger in America
Malnutrition in a Third World Community
Nails
Organic Farming: Can It Feed the Multitudes?
Population Explosion (1959)
Population Explosion (1967)
Population Time-Bomb
Projection '70: Food Production
The Quest for Food Series (Five 29 min. video cassettes produced by Penn State in 1977)
Rice
Sorry, No Vacancy
3900 Million and One
A Tale of Three Cities
Tilt
Toast
Tragedy or Triumph
Will the Fishing Have to Stop?
World Food I

"APPROPRIATE TECHNOLOGY"

Backyard Alternative Energy
Bates Car: Sweet as a Nut
To Build a Pollution-free Car
A City Farmstead
Down to Earth: City Living
Farming with Nature
The New Alchemists
A Place to Live
The Power to Change
The Solar Promise
Waste: Penalty of Affluence
Waste: Recycling the World
Wastewater Bonanza

ENERGY

Coal
Coal: Solution or Pollution?
Dawn of the Solar Age: Solar Energy
Dawn of the Solar Age: Wind and Water
Energy: A Conversation
Energy: A Matter of Choices
Energy: An International Crisis
The Energy Carol
The Energy Connection
Energy Crisis
The Energy Crisis Series (Seven "NBC White Papers" which comprise a three hour documentary as shown on television in 1973)
Energy: Critical Choices Ahead . . . A New Look
The Energy Crunch: The Best Way Out
The Energy Crunch: The Nuclear Dilemma
The Energy Crunch: The Sunbeam Solution
Energy: The Dilemma (Second Edition)
Energy: Fuels and Man
Energy for the Future
Energy from the Day Star
Energy: Innovative Alternatives
Energy: Less is More
Energy: The Problems and the Future

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Energy: New Sources (2nd Edition)
Energy: The Nuclear Alternatives (2nd Edition)
Energy Seekers
Energy: Toward the Age of Abundance
Energy: What About Tomorrow?
Focus on Energy Conservation
Focus on Energy: What are our Choices?
Focus on How Much Gas and Oil Do We Have?
Fusion: The Energy Promise
Future Fuels
Gambling With Our Lives
Geothermal: The Energy Within
The Global Energy Game
Incident at Browns Ferry: Parts 1 and 2
The Invisible Flame: Parts 1 and 2
Joey's World
Lovins on the Soft Path
Natural Gas
No Act of God
Nuclear Energy: The Question Before Us
The Other Way
Power
The Power Game (Oasis in Space Series)
Solar Energy: The Great Adventure
The Solar Frontier
The Sun: Its Power and Promise
Terraset Sun
Thine is the Power: A Citizen's Guide to the Nuclear Energy Debate
A Thousand Suns
We Will Freeze in the Dark
When the Circuit Breaks . . . America's Energy Crisis
Which Energy?

MISCELLANEOUS

Appalachia: No Man's Land
Appalachia: Rich Land, Poor People
Automania 2000
Black Coal-Red Power
Boomsville
Botanic Man #8: On the Limit
Botanic Man #10: Crackpot Jackpot
Bulldozed America
Chain of Life
Cities in Crisis: What's Happening . . . ?
The City
City Limits
Computology: Preventing Eco-collapse
Conservation and Balance in Nature
Conservation Down on the Farm
Conservation Road
Ecological Biology
Ecology: Barry Commoner's Viewpoint
Ecology: The Silent Bomb
E. F. Schumacher . . . As If People Mattered
The End of One
Environment
Farming With Nature
The Finite Earth Series (Four 29 min video cassettes produced by Penn State Television in 1978)
Fires of Spring
Focus on the Environment
Gambling with Our Lives
The Garbage Explosion
Have Our Planet and Eat It Too?
House of Man, Part 1: Our Changing Environment
Industrial Britain
Interview with Garrett Hardin
Junkdump
Land Use and Misuse
Law of the Land
Limits to Growth (Edited Version)
Look to the Land
Look What We've Done to this Land
Man and the "Second" Industrial Revolution
Mission Possible, Part III: They Care for a Nation
Mountain Music
Multiply . . . and Subdue the Earth
Once Upon a Wilderness
Pandora's Easy-Open Pop-Top Box
Pave It and Paint It Green
Planning the Land
The Ravaged Earth
The Ravaged Land
Rich Man, Poor Man: Food
River (Planet Earth)
Room to Breathe
Seeds of Destruction (Living Earth Series)
Self Service
The Stationary Ark: How Dead is Dead?
The Stationary Ark: Surviving
Strip Mine Trip
Technology and Values: The Energy Connection
This Vital Earth (Living Earth Series)
Time for Survival
The Tragedy of the Commons
The Turtle People

To Defeat the Doomsday Doctrine (Target The Impossible Series)
Up to our Necks: The Garbage Problem
Urban Ecology Series (Three 15–20 min films produced by CBL)
Use It, Use It Up
Visions of Tomorrow (Oasis in Space Series)
Water Famine
Web of Life
Yours Is the Land

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Science as a Way of Knowing—Human Ecology[1]

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SYNOPSIS. This essay is part of the second presentation of an educational project of the American Society of Zoologists. The purpose of the project is to offer suggestions for improving the first-year biology courses in the universities. The method consists of emphasizing the conceptual framework of the biological sciences, showing how scientific information is obtained and evaluated, pointing out the strengths and limitations of scientific procedures, and above all showing the relevance of science for human hopes and welfare. Each year a major topic will be considered. Last year it was *Evolutionary Biology*. This year it is *Human Ecology*.

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[1] From the Symposium on *Science as a Way of Knowing—Human Ecology* presented at the Annual meeting of the American Society of Zoologists, 27–30 December 1984, at Denver, Colorado.

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RATIONALE FOR THE PROJECT

Why we need to do something

In a recent editorial Morris H. Shamos (1984), Professor of Physics at New York University, wrote, "Currently, all that is really accomplished by requiring science in high schools and colleges is to maintain the size and the variety of our science departments." That statement may have an element of hyperbole but it surely has an element of truth. But the most astonishing thing is that, in this Age of Science, it can be said at all. The most hopeful word in the quote is "currently," since it implies a transitory state—science courses were considered educationally valuable in the past and can become so in the future.

Shamos' evaluation is shared, to varying degrees, by many. If we restrict ourselves to the college and university level, it must be admitted that many courses and textbooks tend to be fact-laden encyclopedias testing the student's ability to survive rather than providing a deep and satisfying understanding of the natural world. The familiar argument (excuse) is that it is necessary to provide the student with the basic names and facts that must be mastered before advanced courses are undertaken. Another familiar pattern of instruction, especially in the biological sciences, is to emphasize the glamour of recent research to a body of students almost totally unable to appreciate the significance of what is being presented. Physicists and chemists do not make this mistake.

For many students the first-year course is both the beginning and the end of their exposure to science. The inadequacy of many courses in science is coming to be recognized as a problem of nationwide significance. The flurry of recent reports on the "educational crisis" have all stressed the importance of improving the teaching of science and mathematics. Congressman Mike McCormack (1983) speaks of the need to "break the existing condition in which unqualified teachers are passing on to uninspired students unacceptable attitudes toward an understanding of science and mathematics."

There are valid reasons for this concern. The nation must have a constant flow of educated and disciplined minds to staff the offices of government and business, manage the factories, heal the sick and litigious, build the X-generation computers, defend the nation, augment our culture, and win the Nobel Prizes. But there is another reason—equally important when we remember the first mission of higher education. Science is an intellectual enterprise with a beauty, importance, and relevance that makes it one of the most notable achievements of mind and civilization. A course in science must become an intellectual adventure for the student and a basis for a thoughtful, contributing, and rewarding life in society. Ralph Stocking (1984), in a recent and very personal essay, tells what science means for him.

Today our world is so complex that, not only is ignorance of science life-threatening for the nation, but it is life-threatening for the individual as well.

The general perception that biological education in the colleges and universities fails to meet the needs of students and of the nation is the stimulus for the *Science as a Way of Knowing* project of the American Society of Zoologists and nine other professional societies. Most members of these societies teach at the college or university level—the level for which they are responsible and are in a position to attempt remedial action.

The many recent national studies of the "crisis in education" have focused mainly on the precollege years and are strangely silent about higher education. Yet a strong argument can be made that the colleges and universities are a central element of the problem and, hence, must be central in any solutions. The universities define the academic disciplines, are foremost in adding to them, and they transmit much of the knowledge—especially at an advanced level.

A key responsibility of the colleges and universities is to select, educate, and attest to the competence of those students who will become the teachers in the schools. It is not unreasonable to suggest that any long-term solution of the crisis of education in the precollege grades cannot occur until

the colleges and universities take more seriously their responsibility for the education of those who will teach in those grades. Recently Arons (1984) has expanded this topic.

Science as a Way of Knowing was launched at the December 1983 annual meeting of the American Society of Zoologists. Our general plan is to present at each annual meeting one broad topic. Last year it was "Evolutionary Biology." This year it is "Human Ecology." In 1985 we have scheduled "Genetics" and in 1986 "Developmental Biology." We should complete the major topics of biology in eight to ten years and, if the project is judged to be useful, the cycle will then start over.

The events at each annual meeting consist of two half-day symposia, a film program, and the distribution of a long essay, an example of which you are now reading. The proceedings for *Science as a Way of Knowing—Evolutionary Biology* were published in the May 1984 issue of the *American Zoologist* (24:419–534).

What we are trying to do

Our suggestions for how science should be taught in the colleges and universities do no more than emphasize what has been traditionally thought of as good teaching. We stress that the most important emphasis should be given to the conceptual framework of the field. The basic concepts of the field allow the scientist and the student to arrange the data derived from observation and experiment in a rational order and provide also a powerful mnemonic device. The student gains both facts and understanding.

Two generations ago Leslie A. White (1938) had this to say:

> Science is not merely a collection of facts and formulas. It is preeminently a way of dealing with experience . . . . Science is one of two basic ways of dealing with experience. The other is art . . . . The purpose of science and art is one: to render experience intelligible, i.e. to assist man to adjust himself to his environment in order that he may live . . . . Science deals with particulars in terms of universals . . . . Art deals with universals in terms of particulars . . . . Art and science thus grasp a common experience, or reality, by opposite but inseparable poles.

The facts of science will be better understood and placed in perspective if the student is made aware of the question being asked or the hypothesis being tested. This is usually so self-evident to the teacher that it might not seem necessary to mention it to the student. It is astonishing how much of the science that is taught consists only of answers and how little spirit of scientific inquiry reaches the classroom.

It is important to emphasize that science as a way of knowing is but one way of knowing. What we know in science must be based, in the final analysis, on data derived from observation and/or experiment relative to some natural phenomenon. Those data must be obtainable by all competent scientists, hence be verifiable. Statements based on data that can be confirmed become part of the corpus of science; statements that cannot be confirmed must be modified or rejected. Scientific procedures make the quest for understanding the natural world a self-correcting process. This understanding becomes ever more precise as it is constantly purged of ignorance and error. This understanding becomes a thing of beauty and awe as the incredible complexity of the natural world is translated in a script that can be mastered by the human mind. One should not speak of "ultimate truth" in science but of statements that are ever more comprehensive in describing natural phenomena and ever more useful in predicting what is yet to occur.

There is another way of knowing, seemingly with greater appeal for the human mind, where answers are accepted on the basis of emotion, revelation, inspiration, adherence to dogma, or the opinions of others. Included here, as mentioned by White, is the world and experience of art. The prime example of this non-scientific way of knowing is religion, where knowledge is equated with faith.

Different minds view these two approaches to knowing differently. Some-

times they are characterized as the way of the mind and the way of the heart. One can—must, I should think—present and compare the two points of view to students without disparaging either. But having done that, it is not unreasonable for a teacher to explore the efficacy of the two procedures for answering questions about the natural world and for solving human problems. Is agricultural productivity enhanced more by science or by faith? Is sickness cured more by medical science or by faith? For the first one can exclude faith; for the second both may play a role.

It is important to emphasize how very few important human questions can be answered, or human decisions reached, solely on the basis of scientific information and procedures. Both the questions and the decisions are more likely than not to involve emotion, preference, and the ethics, traditions, and aspirations of the tribe. What could possibly be the scientific reasons for decisions to feed the hungry or cure the sick? Nevertheless, once a human and humane decision has been made, for these or other matters, scientific data and procedures might be the *sine qua non* for achieving the desired results.

If developing the conceptual framework of the field becomes the major thrust of a first-year science course, there are several desirable consequences, apart from the value for the course itself. A conceptually-rich course may prove to be more appropriate for non-majors than a facts plus vocabulary approach. It is probable that a conceptually-based course might stimulate students who never intended further work in science, especially the more gifted, to continue the study of science. We have all known of fine students who have been "turned off" by the banality of fact-laden, concept-poor, introductory courses.

It is hard to conceive of approaches that would produce a first-rate course for non-majors that would not also be superior for majors (an argument extended in J. A. Moore, 1983). A concept-rich first-year course also has great benefits for the advanced courses in the department since the advanced courses can build on a working knowledge of biological concepts and processes.

An introductory course that stresses only the modern developments will have an audience largely unable to understand the importance of those developments. Modern developments have their greatest usefulness in supporting, extending, and improving the conceptual framework of a field of science and when dealt with in a course must be in relation to that framework. An important discovery made in 1984 may be of greater interest to a scientist who knows why it is important than a discovery made in 1884 or even 1974, which the scientist has already integrated into his or her conceptual framework. The same is probably not true for the student who has not heard of any of the three discoveries, and it could be that the discovery of 1884 is more seminal than the others.

Structure of the argument

One idealizes the form of a scientific argument by recognizing first, a question to be asked about a natural phenomenon; second, using the available information to suggest a provisional answer (the hypothesis); and third, testing deductions from the hypothesis.

That formal procedure was followed closely in last year's essay (J. A. Moore, 1984) when the topic was Evolutionary Biology. A somewhat different procedure will be followed for this year's Human Ecology essay. This will not be because evolutionary biology is "scientific" and human ecology is not, but because the major hypothesis of ecology, and its test by deductions, was made by our ancestors no later than the Old Stone Age.

The fundamental hypothesis of ecology is that there are interrelations between organisms and their environments. These interrelations are so obvious—the roles of food and other molecules, a place to live, climate, other organisms, etc.—that they are accepted without argument. On a more elegant level of analysis we can say, once we understand that living organisms require but create neither matter nor

energy, that the environment must be the only source.

Thus in developing the topic Human Ecology it will be assumed that, beyond all reasonable doubt, organisms interact with their environment, and our task is to inquire about the nature of that interaction. This inquiry will involve many instances where the hypothetico-deductive procedures will prove to be powerful devices for answering questions, but Human Ecology cannot be presented in as structured and conceptually rigorous a manner as, for example, can evolutionary biology or genetics.

The intended audience for the *Science as a Way of Knowing* project is our colleagues in biology departments of colleges and universities, and especially colleagues who have the responsibility for first-year courses. The amount of material that will be discussed in this essay is far greater than would be appropriate for a year's course that has to consider all the major subfields of biology. It must be remembered, therefore, that the purpose of the essay is to provide a framework of information and understanding of ecology and so provide a more secure intellectual base for what is chosen to be presented in classroom, field, and laboratory.

And, as always, criticisms and suggestions will be much appreciated. This must be a cooperative effort if we are to do our part in achieving sustainable reform of the nation's educational system.

And I must enter a disclaimer about the use of apparently sexist terms. "Man" has become a pejorative term in the eyes of some and for that reason I have very much reduced its use. There are times, however, when it becomes awkward to substitute "men and women," "human beings," "shims," "males and females," or whatever. For centuries "man" has been used as a synonym for "human being" and that is the way I am using it.

The references

There was general approval for the large number of references provided in last year's essay (J. A. Moore, 1984) so there is a large number for this essay as well. Included are the ones that I have found interesting and useful. They range from elementary introductions to advanced monographs. The time available for preparing this essay (four months) did not permit a systematic review of the literature to find the "latest and the best." I did not fret over this limitation because what might be "best" for me need not be so for another. In some instances I have placed an * by titles that can serve as useful introductions to the topic and its literature.

If I were asked to name a few books that would be most useful for the *start* of a personal library, the list would be Paul Ehrlich, Ann Ehrlich, and John Holdren (1977), C. D. Darlington (1969), John Gowlett (1984*a*), Jacquetta Hawkes and Sir Leonard Woolley (1963), Eugene P. Odum (1971), and J. Z. Young (1971).

Many of the books were originally published in foreign countries but, if the publisher indicates an office in the United States, that alone has been noted in the list of references. I have tried to list the first name, rather than only the initial, for authors of books even if such information is not given on the title page. The purpose is to lessen the problem of finding the title in the library's card catalog. I have included a few references that appeared from the title to be important but that I was not able to check. Forgive me if the citation is in error.

I. THE FUNDAMENTALS OF ECOLOGY

In this section some of the fundamental principles of ecology that apply to all organisms will be considered. This will provide the background for the major topic, Human Ecology. Such a background is essential. Our mostly urban population frequently overlooks the basic biological fact that we are an integral part of nature and must abide by its laws that regulate the lives of all animals and plants. Once we are done with the fundamentals, we will consider Human Ecology from two points of view. Part II will deal with the main ecological problems that confronted the human population from the Paleolithic

Period to recent times. Part III will deal with today's ecological problems, which are among the most important things there are for us to think about.

As a first question to consider, you might have your students list all the environmental factors they can think of that influence organisms one way or another and suggest the consequences of these influences and the relative importance of each. The importance of asking students questions is not only to obtain answers but to make them think about the problems. In addition, you will gain important insights into the students' level of understanding of ecological interrelations.

One of the most basic principles of ecology, again so well understood that it seems trivial to mention, is that the behavior of all living organisms is directed towards securing the necessities of life from the environment for reproduction and for avoiding death. That is, behavior is a life-continuing and life-preserving activity. It could hardly be otherwise: the twin forces of variation and natural selection must favor those genotypes that enhance fitness.

The evolutionary process has resulted in innumerable solutions to this basic problem of trying to stay alive and reproduce. Each distinctive solution is a unique species.

Each individual organism has a complete or partial ability to secure the resources needed for life. The individuals of most species spin out their lives with few interactions with others of their species apart from events related to sexual reproduction. The social species, on the other hand, have evolved behavior patterns that allow them, through social interactions, to secure resources and protection more readily. These patterns, complex in many of the insects, reach a peak in our species. Today few human beings can or do live wholly independent lives. The chances for survival and the ability to obtain resources increase progressively with the family unit, the tribe or village, the city, the state, and the nation.

The special case of human ecology will be treated in Parts II and III but this Part will deal with the general principles of ecology that will enable us to understand ourselves. We will start by considering some of the ecological problems of maintaining life in an autotrophic flowering plant, a heterotrophic animal, and biological communities.

The flowering plant way of life

Primitive human beings must have observed what appears to be a fundamental difference in the material requirements of animals and green plants. Animals seemed to devote much of their time searching for food and eating it. Green plants would have appeared to require very little from the environment.

Jean-Baptiste van Helmont (1577–1644) proved to his satisfaction that green plants require only water. In a famous experiment he planted a small willow tree, weighing only five pounds, in a container with 200 pounds of heat-dried earth. The container was covered to keep out dust. He allowed the tree to grow for five years while adding only pure water (rain or distilled) to the container. At the end of the experiment he removed the tree, roots and all, and found that it weighed 169 pounds—an increase of 164 pounds. The soil was lighter by two ounces—a trivial loss. Since only water had been given the plant, the leaves, roots, trunk, and branches must have been formed from the water (Gabriel and Fogel, 1955, p. 155; Schwartz and Bishop, 1958, pp. 199–200).

For a substance as simple as water to form such complex structures as the parts of a plant may seem like a remarkable conversion. Yet in van Helmont's time water was not thought of as the simple substance we recognize today. Water was one of the four basic "elements" of which all matter was formed. The other three were earth, fire, and air. Hence it was not surprising that water could exist in a myriad of forms.

Essential elements

The overwhelming importance of plants for human life made it essential for farmers and scientists of long ago to learn as much as they could about crop plants. The farmer might obtain good crops for several years, then observe a slow decline. Some farms produced good crops; others gave a much

lower yield. Substances such as manure or crushed mollusk shells might improve the soil's fertility. The use of the word "fertility" suggests that the soil was producing offspring—the crops.

For most of history, hunger has been an ever-present feature of human life. Thus, it was of the greatest importance to discover the nature of soil fertility. What did soil give to the plants and, if this gift was exhausted, could something be added to restore the fertility of soil? Clearly the substance of the plant must come from the environment, and the material environment was soil, water, and air. When these questions were first asked there was not enough knowledge of chemistry to provide an answer. When plants were burned, water vapor was expelled and a charcoal-like material was left. The charcoal could be burned again and a small amount of ash remained—which was assumed to be mainly mineral matter. So it was concluded that the substance of plants consisted of water, charcoal or what we would now call carbon, and minerals.

As the science of chemistry slowly developed, it became possible to identify more and more substances and to detect them in ever smaller concentrations. With the methods available today it is possible to ask the question "What are the chemical elements that a green plant obtains from the environment that are essential for its growth and development?"

Note the word "essential" in the question. There are important differences between a substance occurring in an organism and its being essential for life. Our bodies, for example, have a diverse inventory of chemical substances such as DDT, mercury, lead, dioxin, and PCBs that are not exactly required for our growth and well being. Plants have all the elements present in the soil in which they grow but not all are essential.

The problem of determining what a plant requires is far more subtle and difficult than it may seem. You might wish to have your class propose experiments designed to answer this question: How does one establish which substances in the body of a green plant are essential and which are contaminants? In much the same way that Koch established the postulates for proving that a specific microorganism is the cause of a specific disease, Arnon and Stout (1939) suggested criteria for establishing whether or not an element is essential for the life of a plant:

> an element is not considered essential unless (a) a deficiency of it makes it impossible for the plant to complete the vegetative or reproductive stage of its life history; (b) such deficiency is specific to the element in question, and can be prevented or corrected only by supplying this element; and (c) the element is directly involved in the nutrition of the plant quite apart from its possible effects in correcting some unfavorable microbiological or chemical condition of the soil or other culture medium.

to which Price (1970, p. 203) adds,

> a nutrient is also essential if it is an indispensable part of an indispensable component of the organism.

As research continued on the elements required for the growth of plants it became clear that some elements are essential yet are required in exceedingly small amounts. The standard experimental procedure to test for essentialness is to grow plants in an artificial medium composed of distilled water and various "pure" chemicals in order to see which are needed. The problem is that neither pure water nor pure chemicals exist. Your students might be surprised if they look at the analysis data on the bottles of the best grade reagent chemicals.

The problem of contamination might be exceedingly subtle. For example Arnon and Stout noted that copper appeared not to be an essential element for tomatoes when they used distilled water from a conventional still (with metal parts). However, when that water was redistilled several times in a Pyrex glass still, copper salts had to be added to the nutrient medium for normal growth. So Arnon and Stout realized that the operational criterion for an element being essential must be "whether the plant requires it in an amount greater

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than that present in the culture medium as a result of contamination."

Arnon and Stout's paper can be used to emphasize to students an exceedingly important principle of scientific methodology: *in science one can do no more than approach a "true" answer.* Their very short paper can serve as a model for scientific procedures and is written at a level that can be understood even by students in first-year courses.

When the chemicals and distilled water of the late 19th century laboratories were used to prepare the artificial salt solutions to ascertain which elements were essential, very few appeared to be required. As the purity of reagent grade chemicals improved, the list began to grow and it was found that many elements were required in trace amounts. Today the "sure" list numbers 16 (Table 1) but, as we will see, there are some probable additions.

Consider with your students how one might go about proving that a list of 16, or whatever number, is complete. How could one prove that an element is *not* essential? Arnon and Stout leave open the possibility that each and every one of the naturally occurring elements may be shown eventually to play an essential role in some or all green plants.

TABLE 1. *The elements essential for green plants.*

A. The nine elements found in the highest concentrations.

Element	Percent (wet weight)
Oxygen	86.65
Hydrogen	10.90
Carbon	2.25
Nitrogen	0.075
Potassium	0.050
Calcium	0.025
Magnesium	0.010
Phosphorus	0.010
Sulfur	0.005
Total for the above	99.975

B. Trace elements each occurring in concentrations of less than one thousandth of a percent.

Chlorine	Iron	Manganese	Boron
Zinc	Copper	Molybdenum	

C. Other elements which are important in some green plants.

Silicon.	A structural component of grasses and horsetails.
Cobalt.	A component of vitamin B_{12}.
Sodium.	Appears to be essential for some plants living on saline soils, especially those with C_4 metabolism.
Selenium.	Accumulated in some plants and may be required.

Note: The dry weight values have been adjusted to apply to a plant with a water content of 95 percent.

The elements essential for green plants (Table 1) are required in very different amounts. Oxygen, hydrogen, and carbon comprise 99.8 percent of the plant. They are obtained from carbon dioxide, which enters through the stomata, and water, which enters mainly through the root hairs. The remaining 13 essential elements enter through the roots primarily as inorganic molecules.

There are some wonderful stories about the quest for essential elements, in addition to that of copper which has already been told. Chlorine is now known to be essential for photosynthesis, as was shown by Broyer *et al.* (1954). Earlier work suggested that chloride ions might be essential, so Broyer and others in P. R. Stout's laboratory at the University of California at Berkeley began to study the problem. As usual, the experiments were conducted with water and chemicals made as pure as possible. At first plants growing in solutions without detectable chloride seemed to suffer no ill effects. But what about the work of others that hinted at a need for chloride? Someone in the lab remarked that the air had not been excluded as a source of chloride. The Berkeley campus is near the Pacific Ocean and almost every day the fog rolls in. To test the hypothesis that traces of chloride were carried in the air, special filters were used for the experimental chambers. Thereafter, plants grown in the purified solutions did poorly but became healthy when trace amounts of chloride were added.

There are several morals to this story, told to me by Dan Arnon. First, it shows what extraordinary care scientists must take to do the experiment they think they are doing. Second, it shows how careful one must be when working with tiny amounts of materials. Third, the environment may

TABLE 2. *Corn metabolism.*

Production

One acre of good farming soil may produce 100 bushels of corn.

The total amount of plant material, air dried, will consist of:

5,600 pounds of shelled corn	1,400 pounds of cobs
5,200 pounds of roots and stubble	4,000 pounds of stalks

Of the total of 16,200 pounds, the shelled corn represents 35%.

Consumption

To produce this amount of corn, the following raw materials must be obtained from the environment:

Water	5,000,000 pounds	Sulfur	22 pounds
Oxygen	6,800 pounds	Magnesium	33 pounds
Carbon dioxide	19,000 pounds	Calcium	37 pounds
Nitrogen	130 pounds	Iron	2 pounds
Phosphorus	22 pounds	Manganese	0.3 pounds
Potassium	110 pounds	Boron	0.06 pounds

And trace amounts of:

Chlorine	Iodine	Zinc	Copper	Molybdenum

Energy

And during the year the acre would receive between 2 and 4 billion kilocalories of light energy but the amount used by the corn plants would be half or less of the total amount.

include features not usually recognized. Fourth, it shows the near impossibility of proving that a phenomenon cannot exist.

Nutritional deficiencies

Not all elements now known to be essential were discovered by systematic laboratory work. Some were discovered when crops growing on certain soils were found to be abnormal. One could test the hypothesis that this was due to insufficient amounts of some element by systematically adding one or more presumed to be lacking to the soil. If growth were normal, that would be the first step in establishing the existence of a new essential element. Confirmation would come with carefully designed laboratory experiments.

Thus "potato sickness" in Maine's Aroostock County was found to be cured by adding traces of magnesium; "blossom end rot" of tomatoes by adding calcium; and "cracked stems" of celery by adding a trace of boron. Different diseases of citrus have been linked to deficiencies of the soil in nitrogen, phosphorus, potassium, calcium, magnesium, zinc, manganese, copper, iron, boron, and molybdenum. Of all the trace elements, molybdenum is the one required in the smallest quantities, yet at times the soil cannot supply even this in adequate amounts. Boron is also required in minute amounts, yet boron deficiency is a worldwide problem for many crops.

The presence of an element in the soil does not insure its availability to plants. Iron is almost always abundant—the top 15 cm (6 inches) of a hectare (2.5 acres) might have as much as 45,350 kilograms (50 tons) of iron. Nevertheless, in a neutral or alkaline soil the iron compounds are so insoluble that they are unavailable in adequate amounts for green plants. Useful references to deficiency diseases in plants are Barber *et al.* (1964), Wallace (1953), and M. J. Wright (1976).

Recipe for making corn

Sprague (1964) estimated the quantities of raw materials that are required for the production of corn and his data are summarized in Table 2. The total required to produce 5,600 pounds of shelled corn is a staggering 5,026,157 pounds of raw materials. Expressed in another manner, it requires about 900 pounds of raw materials to produce a pound of shelled corn, which can serve as food for man or beast. In addition, cattle can eat the stalks. Or we could say that only 0.1 percent of the raw

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materials becomes converted to human food—which goes to show that it takes a lot of environment to support a heterotroph, especially one that feeds wholly or in part on other animals.

It might be interesting to ask your students why nutritional deficiencies are so common in crops, yet are infrequent in wild species. If the answer is not forthcoming, asking "Why is it necessary to fertilize crop land?" may do the trick. Such a discussion will set the stage for a later consideration of cycles and the chemical balance in natural communities.

Some useful references on the chemical requirements of green plants are Arnon and Stout (1939), Barber (1964, 1984), Bidwell (1979), Bollard and Butler (1966; a review of the elements with a questionable status), Bonner and Varner (1976), *Clarkson and Hanson (1980), Devlin (1975, chs. 13–16), Epstein (1972, 1973), H. J. Evans and Sorger (1966), Galston, Davies, and Satter (1980), Gauch (1972), Läuchli and Bieleski (1983), Mortvedt *et al.* (1972), Price (1970), Rains (1976), Salisbury and Ross (1978), *Ting (1982), and Wyn Jones and Lunt (1967). Here and throughout, references that provide good introductions are marked with an asterisk.

Energy for making corn

The molecules of Table 2 cannot put themselves together and produce an acre of corn plants. The molecules of that list have low chemical potential energy whereas the organic molecules of the corn plant have high chemical potential energy. The conversion of molecules with low chemical potential energy to molecules with high chemical potential energy depends on the synthetic mechanisms of the chlorophyll-containing plant cells driven by the energy of sunlight. Thus, the development and growth of the green plant involves a decrease in entropy of the molecules it acquires and synthesizes into complex carbon compounds. If entropy is to be decreased, energy is required.

If students are not already familiar with that fundamental constraint on living systems, the Second Law of Thermodynamics, this would be an appropriate place to provide a very brief introduction. A question to the class should find some students who can explain this fundamental law that sets the limits of what living and nonliving nature can do. For more details see Morowitz (1970), and Ehrlich, Ehrlich, and Holdren (1977, pp. 33–35).

Apart from chemosynthesis by bacteria (as in the thermal vents), trivial amounts of energy from thermonuclear reactions and from celestial bodies other than the sun, the energy for living activities is derived solely from the sun. Most of this energy is from sunlight received currently but many human activities depend, directly or indirectly, on the energy of ancient sunlight, trapped by green plants and stored in coal, oil, and natural gas, or on that energy of sunlight used in the evaporation of water which, when deposited as rain at high elevations, can be used to generate hydroelectric power as it flows downhill.

The importance of sunlight in the production of food by green plants is so great and so spectacular that we tend to overlook another equally important role of the sun's energy—to provide a moderate temperature environment. If somehow the sun were turned off, the temperature at the earth's surface would drop to very near absolute zero (−273°C). At such temperatures the chemical interactions that are life could not occur. In fact, for most organisms these reactions cannot occur at temperatures that approach 0°C. Thus the warming effects of sunlight are essential for photosynthetic reactions.

Photosynthetic reactions use sunlight in quite a different manner. Light energy, instead of being converted to heat, is converted to chemical energy stored in organic molecules such as carbohydrates, proteins, and fats. The details of photosynthesis are not part of ecology, which is a "skin out" part of biology, and need not be further considered here. There are however some other important things to be said about sunlight.

The light used in photosynthesis is mainly that part of the electro-magnetic spectrum detected by the human eye, that is, extending from relatively short wavelength ultraviolet to the longer wavelengths near

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infrared rays. In photosynthesis the maximum absorption is in the blue and red ends of the visible spectrum. Green light is reflected, which is why we see plants as "green." It is interesting to note that the human eye is most effective in bright light at 556 nm, which is yellow-green.

A truly trivial fraction of the sun's total energy reaches the earth. Our world would appear as a tiny disk if viewed by an observer on the sun. Your students can confirm how small the amount is by determining how the area of a disk (circle), with a radius of 6,375 km (the radius of the earth) compares with the surface area of a sphere with a radius of 149,500,000 km (mean distance from the earth to the sun). (Area of a circle = 3.14 × radius^2. Surface area of a sphere = 12.57 × radius^2.)

A tremendous amount of energy is released in the sun when hydrogen combines to form helium and it starts the long journey to us as light, but only a very small amount of this energy becomes available for living organisms. E. P. Odum (1975, ch. 3) provides a synopsis of what occurs. At any one time only half of the earth is illuminated. Taking this into consideration, the theoretical amount of light energy that approaches the earth is about 5,250,000 kcal per square meter per year. Yet not all of this reaches the earth's surface. Much becomes heat in the atmosphere. Clouds and dust further reduce the amount to between 20 and 40 percent of the original.

If we apply these data to that acre of corn (Table 2) we must remember that the plants will be growing for only part of the year so the sun's energy at other times will not be captured by food plants.

We can determine how many kilocalories of light energy are required to produce a kcal of corn plant and of human food. The acre produced 16,000 pounds of dry weight corn plant. This is equal to 7,258 kilograms. An acre contains 4,050 square meters. Therefore each square meter of a cornfield produces 1.79 kilograms of dry weight corn plant. If we assume that each gram of corn plant contains 3.8 kcal, a square meter will have produced 6,802 kcal of food for the year. This is only 0.13 percent of the 5,250,000 kcal per square meter of light energy that would reach the earth each year in the absence of clouds, dust, etc. But most of the light is reflected or becomes heat. In fact only about 500,000 to 1,000,000 kcal per square meter would actually reach the corn plants and produce those 6,802 kcal of food. This means that between 0.68 and 1.36 percent of the available light energy is captured. Since the shelled corn represents 35 percent (Table 2) of the plant material, only 0.24 to 0.48 percent of the energy of sunlight becomes the energy of human food.

Corn, we might add, is one of the most efficient captors of solar energy among the food plants. Woodwell (1970) estimates that only about 0.1 percent of the sun's energy is fixed in photosynthesis.

We must add the energy required for that acre of corn to the figures in Table 2. When the 500,000–1,000,000 kcal of light reaching each square meter per year are adjusted for one acre, the energy reaching the plants and available for their growth becomes 2,025,000,000 to 4,050,000,000 kcal. Remember that the growing season does not occupy the entire year but, even if we correct this by dividing by two or three, we still have very large numbers. Although a very large amount of energy is available, only a fraction is used by the plants.

Some references to this aspect of the green plant way of life are: Bainbridge *et al.* (1966), Bickford and Dunn (1972), Clayton (1970–1971), G. C. Evans *et al.* (1975), Gates (1962, 1963, 1980), Gates and Papain (1971), *Janick *et al.* (1981, ch. 2), E. P. Odum (1968; *1971, ch. 3; *1975, ch. 3), H. T. Odum (1971), Oster (1968), Seliger and McElroy (1965), *Ting (1982, chs. 3 and 7), Townsend and Calow (1981), Whittaker and Likens (1973), Woodwell and Whittaker (1968).

A place to live

Life for green plants is more than sitting in the soil soaking up sunlight, carbon dioxide, and minerals. The pressures of natural selection, acting over the ages, have tended to make every species a rigid specialist. Each comes to possess an almost

unique way of life that is called its "niche." Niche is used in two main ways: a place to live or a way to live; the second definition will be used here. The specific way to live is correlated closely with a specific place to live, which is the topic of this section.

The surface of the earth exhibits a great diversity of environments; polar and tropical; rain forest and desert; lakes and oceans; soil and bare rocks; land and air; mountains and valleys. No species is at home in all of these; most have evolved to live efficiently in a specific and relatively constant environment. Species are specialists of the particular, not tolerants of the general.

Even in the eastern United States, where there are relatively few abrupt changes in the environment over short stretches of latitude or altitude, except where land meets water, the species of green plants tend to be restricted to relatively small geographic areas. Within these small geographic areas species will occur in spots determined by the types of soil, water, slope, other organisms, the availability of light, and the strength of the wind. West of the Great Plains the environmental changes tend to be abrupt and the geographic ranges of species tend to reflect this fact.

If species have evolved for specific environments, one might hypothesize that similar environments will have the same or similar species (assuming that dispersal among these similar environments is possible). We do find that there are rules that describe the geographic distribution of green plants that are correlated with the three major environmental influences: temperature, water, and soil. The ubiquity of light, oxygen, and carbon dioxide means that we can take their presence in all land environments for granted.

A historically important investigation of the factors that control the distribution of North American green plants was done by C. Hart Merriam (1890) on San Francisco Peak in northern Arizona, just south of the Grand Canyon of the Colorado River.

San Francisco Peak is an isolated mountain that rises to a height of 3,900 meters (12,800 feet) from a semiarid plateau of about 2,000 meters (about 7,000 feet).

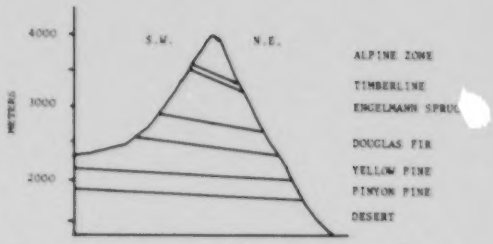

FIG. 1. The life zones of San Francisco Peak. Modified from Merriam (1890).

Thus the height of the mountain above the plateau is about 1,900 meters (one mile). During the summer growing season Merriam estimated that the mean temperature is about 22°C at the base of the mountain and about 4°C at the top.

With this great range of environmental temperatures, one could test the hypothesis that temperatures limit the distribution of the plant species. Since there is a direct relation between altitude and temperature, one could deduce that the various species would be restricted to specific altitudes where they would find the temperature range for which they are adapted. Green plants usually have very effective mechanisms for the dispersal of their seeds, so one would predict that, over time, the seeds of every species on San Francisco Peak would have been deposited at all sites on the mountain. Normal growth and development would be possible, however, only where the acceptable temperatures occur.

After months of studying the plants from base to summit, Merriam was able to reduce his data to a single conceptual scheme. There were distinctive groupings of plant species that formed horizontal bands at different altitudes (Fig. 1).

The plateau at the base of the mountain, at 2,130 meters, is covered by a magnificent forest of Western Yellow Pine (*Pinus ponderosa*), some being as much as 33 meters in height. These form a nearly pure stand up to about 2,500 meters. For an interval of less than 200 meters above this, Douglas Fir (*Pseudotsuga menziesii*) occurs with Western Yellow Pine. Above that, the Douglas Fir forms a nearly pure forest to about 2,800 meters where it is replaced by Engel-

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mann Spruce (*Picea engelmannii*) and Bristlecone Pine (*Pinus aristata*). These two trees occur to an altitude of 3,500 meters, which is the limit for any species of tree on this mountain. This upper limit is known as "tree line" but just below it the dwarf and gnarled spruce and pine form a mat of vegetation about 0.3 meters in height. For the last 400 meters of the mountain crest, above the tree line, there are no trees but some very interesting plants do occur.

Thus Merriam found that San Francisco Peak is characterized by four life zones—three bands of almost pure stands of trees and a treeless summit. There are also unique smaller annuals and perennials for each one of these four life zones. Thus, it seemed highly probable that each life zone represented a specific climatic zone and that the important variable is temperature.

One can test the hypothesis of temperature control by still another deduction. If temperature is the limiting factor for the altitudinal distribution of the plants on San Francisco Peak, the species found at the lower elevations should have a geographic distribution more southerly than the species found at higher elevations. Thus altitude and latitude would be related.

Enough was known about plant distribution in Merriam's time to test this deduction. The Western Yellow Pine extends south into Mexico, occurring at higher altitudes as one progresses south. Ranging north, to southern Canada, it is found at progressively lower altitudes. The other species that are associated with the ponderosa forest have similar distributions.

If we compare the plant species of the ponderosa forest with those that occur above tree line, the difference is striking. The plants of the treeless top of San Francisco Peak have their affinities with the plants of the tundra that borders the Arctic Ocean. This was indeed an astonishing finding. Here in Arizona, with its blistering hot and dry summers, is a vestige of the frozen north. Nine of the species were identical with those collected by the U.S. Army officer and Arctic explorer, Adolphus Washington Greely, at Lady Franklin Bay, which is just west of the northern tip of Greenland and only a few hundred miles from the North Pole. (Greely nearly lost his life on this expedition; most in the party did.)

Figuratively speaking, as one descends San Francisco Peak one travels south from the Arctic Ocean. The plants of the Engelmann Spruce zone are similar to those of the northern half of the great coniferous forest that extends across Canada just south of the northern limit of trees. The species of the Douglas Fir zone have their counterparts in the southern half of this Canadian coniferous forest.

There are other deductions that can be made from our working hypothesis that temperature is an important factor of the environment controlling plant distribution. If this is so, we should expect, other environmental factors being equal, that the boundaries of the vegetational zones on the south side of San Francisco Peak should extend higher than on the north side (ask your students why; the south side is not that much farther south!) Merriam found this to be so (Fig. 1). He found that "the normal average difference in altitude of the same zone on the southwest and northeast sides of San Francisco Mountain is about 275 meters (900 feet)."

Still another deduction would be that, other controlling factors being equal, the plants should occur at lower altitudes as one moves north. This is true. Western Yellow Pine occurs at altitudes from 1,500 to 2,100 meters in the southern part of its range, at 750 to 1,800 meters in the center, and at 150 to 1,800 meters in the north.

Many observations have been combined to give this general rule for the approximate relation of altitude and temperature: for each increase in altitude of 160 meters, the temperature decreases 1°C; or for every increase of 1,000 meters, a decrease of 6°C; or for every 1,000 feet a decrease of 3.5°F.

Temperature is not, of course, the only factor limiting the place where a species lives. The Bristlecone Pine, apart from its occurrence at the top of the tree zone on San Francisco Peak, is found only on a few isolated high mountain tops in California, Colorado, Utah, Arizona, and Nevada at elevations of 2,400 to 3,700 meters. It does not extend to the Canadian tundra. Other

factors must limit its distribution. It is interesting to note that individuals of the Bristlecone Pine are among the most long-lived of all creatures. One tree named "Methuselah" is 4,700 years old. It is located in the Ancient Bristlecone Pine Forest in the White Mountains of California.

Soils, another critical controller of places where plants can live, vary greatly in moisture content, humus, and minerals. The nature of soil becomes especially important if the land is to be used for agriculture. There are many dramatic examples where, other environmental factors being roughly equal, the type of soil controls the distribution and abundance of plant species. We can hypothesize that, since the pressures of evolutionary change result in species being restricted to specific environments, different soil types would be characterized by different associations of plant species.

One dramatic test of this hypothesis is to be found in areas where soil is formed from the disintegration of serpentine rocks (Kruckeberg, 1984*a*, 1984*b*, in press). Such soil tends to be deficient in calcium, sodium, potassium, nitrogen, and molybdenum, all of which are essential for the growth of plants. In addition, chromium, nickel, cobalt, and magnesium may approach toxic concentrations.

In some localities there is a checkerboard pattern of serpentine and more normal soils. In such localities the differences in plant life may be striking. Some serpentine soils are nearly barren; on others the plants are stunted or otherwise abnormal; on still others are species that have evolved an ability to live on soils that are deficient in the elements listed.

One can test the hypothesis that deficiencies of specific elements are the cause of the growth differences of plants on serpentine and nonserpentine soils by adding the needed micronutrients as fertilizers. When this is done, the plants develop normally.

So far as scientific procedures are concerned, botanists did not start with the hypothesis that differences in soils should be reflected in differences in the species of plants. Instead they noticed the abnormal growth and unusual plant associations in some areas. The attempt to find out "why" led to the analysis of soils and the discovery that the phenomenon is associated with serpentine-derived soils.

Every aspect of the environment has its influence on the life of organisms. Deserts and well-watered habitats differ in the species associated with them. The plants on the wind-swept crests of the highest mountains are usually bent and dwarfed. Few species of higher plants find a home in the oceans or in fresh water. Again, evolution promotes the formation of specialists, each restricted to a specific environment. Every spot on earth has a variety of these specialized environments with their unique species and your students should be encouraged to notice this phenomenon where they themselves live. They need not know the names of the species, merely how those of one habitat compare with those of another. Science is not something that is always somewhere else.

General references to plant biogeography and the factors limiting distribution are: Abrams and Ferris (1940–1960), *Daubenmire (1978), Edlin (1973), Eyre (*1963, 1971), Gleason and Cronquist (1964), *Good (1974), Hultén (1964), Jones (1979), Kartesz and Kartesz (1980), Kellman (1980), Kruckeberg (1984*a*, 1984*b*, in press), Livingston and Schreve (1921), McMinn and Maino (1974), Neill (1969), *E. P. Odum (1971, ch. 5), Riley and Young (1966), Stott (1981), and Tivy (1982).

Light: cue to climate

In the temperate and arctic regions, temperature plays a controlling role in the life of green plants. The annuals begin their growth in spring and die as the winter's cold returns. The perennials are dormant during the winter and resume activity with the warmth of spring. One might suspect, therefore, that the slowly increasing temperatures of spring are the cue to start a new cycle of growth and reproduction.

Temperature is a cue but it is not the only one. Temperature would be a reliable indicator of the arrival of spring, and of a safe time to become active, if it increased at a nearly constant rate. This does not happen. Winter and spring are often characterized by alternating warm periods fol-

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lowed by freezes that are lethal to many species of animals and plants. To be adequate an environmental cue must be reliable—and that cannot be said for temperature.

The possibility that light might have a role other than providing energy was first explored in a systematic way by two scientists with the U.S. Department of Agriculture, Garner and Allard (1920). Their investigations were not the result of idle curiosity but a consequence of some puzzling observations that they and others had made.

Years earlier they had observed the strange case of a variety of tobacco known as Maryland Mammoth, so called because at the latitude of Washington, D.C. it grew to a height of 10 to 15 feet. It never blossomed nor produced seeds under field conditions. Seeds would be produced, however, if the plants were transferred to the protection of a greenhouse in the autumn. In addition, seeds planted in greenhouse pots during the winter gave plants that produced seeds after reaching a height of 3 feet—hardly plants of mammoth proportions.

Another observation was that of Mooers (1908; see also Garner, Allard, and Foubert, 1914). He published a paper on soybeans and, as an incidental observation, noted that when soybeans were planted throughout the summer months they tended to blossom at about the same date, regardless of the time of planting.

Garner and Allard (1920) repeated this experiment. They planted seeds of the Biloxi variety of soybeans at short intervals from 9 April through 29 July and observed that all bloomed in September. The 9 April plants began to blossom on 4 September and the 29 July plants on 29 September. This was 148 days for the former and only 62 days for the latter. Furthermore soybeans grown in a greenhouse during the winter "began to develop blossoms before they had anything like a normal growth." Why?

> In seeking a solution of the problem as to why the behavior of these plants is radically different from the normal during the fall and winter months one naturally thinks of light and temperature as possible factors. It was observed, however, that both the Mammoth tobacco and the soybeans still showed the abnormal behavior in the winter even when the temperature in the greenhouse was kept quite as high as prevails out of doors during the summer months. This observation seemed to dispose of temperature as a possible factor of importance in the "winter effect." It is clear that the quantity of solar radiation received by plants is less in winter than in summer, for both the number of hours of sunshine per day and the intensity of light are reduced during the winter months . . . . In the investigation on oil formation in seeds a number of experiments had been made with soybeans to determine the effects of light intensity on this process and, incidentally, it was observed that in no case was the date of blossoming materially affected by the intensity of the light. It has been found, also, that partial shading was without decided effect on the blossoming of the Mammoth tobacco. In view of these experiences it hardly seemed likely that the other primary factor controlling the maximum amount of radiation received by the plant—namely, the length of the daily exposure—could be responsible for the effects in question. Nevertheless, the simple expedient of shortening artificially by a few hours the length of the daily exposure to the sun by use of a dark chamber was tried, and some very striking results were obtained. (Garner and Allard, 1920, pp. 557–558)

Thus their hypothesis was "that the relative length of the day is really a dominating factor in plant reproductive processes" (Garner and Allard, 1920, p. 556). The length of daylight varies considerably at the latitude of Washington where these experiments were done. On 21 June it is about 15 hours; 21 September, 12 hours and 14 minutes; 21 December, 9 hours and 19 minutes.

Garner and Allard used a large light-tight chamber to control the hours the plants were exposed to the sun. The experimental plants were grown in pots and so could be moved easily from open sunlight

TABLE 3. *Garner and Allard's experiments on Biloxi soybeans.*

	Experimental plants			Controls	
Planted	Exposed to sun	First blossoms	Average height (inches)	First blossoms	Average height (inches)
1. May 8–17	10 AM–3 PM	June 16	6–7	Sept. 4	57–58
2. May 8–17	9 AM–4 PM	June 15	11	Sept. 4	57–58
3. June 11–16	6 AM–6 PM	July 14	23–24	Sept. 8	54–55
4. June 14	daylight to 10 AM and 2 PM to dark	Sept. 6	34–40	Sept. 15	47–48

to the dark environment. Control plants were left exposed to the sun. Table 3 summarizes the data.

Those plants with an artificial day length of five hours (10 AM to 3 PM) blossomed in about a month but at a very small size, being only six to seven inches in height. The control group required nearly four months to blossom and grew to 57 or 58 inches. The experimental plants given seven and twelve hours of daylight also flowered rapidly but they produced somewhat larger plants.

Clearly the length of day is important in the relative duration of the vegetative growth and the onset of reproduction in the plant's life cycle. "The term *photoperiod* is suggested to designate the favorable length of day for each organism, and *photoperiodism* is suggested to designate the response of organisms to the relative length of day and night" (Garner and Allard, 1920, p. 603).

The interpretation of the data has, up to this point, emphasized *day*length, that is, the period each day that the plant receives energy from the sun, as the critical environmental influence. This is entirely reasonable considering the absolutely essential role of this energy source in the life of green plants. The Mammoth tobacco and the Biloxi soybeans grew vigorously on a regimen of long days and did not blossom until the days became short in the autumn or were experimentally reduced in length.

But how can one account for Experiment 4 of Table 3 when the period of light was broken by a period of darkness? The total length of the daylight period was 11 hours or less. Why did this way of reducing the length of the light period prove ineffective in inducing early flowering? This puzzle proved to be a clue to a more accurate explanation of photoperiodism.

At this stage in the analysis it would be interesting to ask students if the data of Table 3 can be explained by influences other than day length.

The importance of *light* for plants is so ingrained in our thinking that we tend to overlook the fact that the length of the day has a reciprocal relation to the length of the night. Night and day are the earth's Zero-Sum Game. Mammoth tobacco and Biloxi soybeans are called "short day" plants because they are stimulated to flower normally by the shortening days of autumn. They could be called "long night" plants as well. Experiments 1 through 3 of Table 3 show that blooming is stimulated by days of five to twelve hours *or* nights of twelve to nineteen hours.

Your students should be able to suggest experiments that could distinguish between the controlling mechanism being *day* length or *night* length.

In Experiment 4 of Table 3, the unbroken length of night was the same for the experimental plants and the controls—and the two groups were much alike in the time required to blossom and in the size reached. This is an important bit of information.

An especially instructive series of experiments by Hamner and Bonner (1938) greatly extended our understanding of photoperiodism. They worked with the cocklebur *Xanthium pennsylvanicum*, which blooms when the day length is less than 15.5 hours and the nights have a minimum duration of 8.5 hours. If kept in light for 16 hours in a greenhouse it will grow vigorously but will not blossom.

In a very large number of experiments, Hamner and Bonner showed that the critical factor in photoperiodism was the unbroken duration of the dark period. A brief interruption of the light period, by putting the plant in the dark, was without effect. But in a most dramatic experiment, they broke the dark period by a one minute exposure to bright light. Whereas an unbroken dark period of nine hours would have resulted in blossoming, two dark periods of 4.5 + 4.5 hours separated by one minute of light produced only vegetative growth.

These and a host of other observations have shown that the growth cycle of many plants is dependent on the length of the dark period. Unfortunately the literature still uses the terms "long day" and "short day" plants but the time has come to help students by employing the terms "short night" and "long night" plants. Mammoth tobacco, Biloxi soybeans, poinsettia, chrysanthemums, and many wildflowers that blossom in spring and autumn are long night plants. Radish, lettuce, potato, spinach, other varieties of soybeans, and many wildflowers that bloom in the summer months are short night plants. Some plants, such as dandelions and buckwheat, are said to be neutral—they bloom throughout the warmer months irrespective of the relative lengths of day and night.

The ecological importance of the capacity of a plant being able to recognize the time of the year is obvious. With reasonable accuracy, it must be able to recognize "spring" as a safe time to begin growth. If temperature was the only cue, a warm period during the middle of the winter could mean disaster if the plant ended dormancy and responded by a renewal of active growth. By responding to the relative length of night and day, the plant has a reliable cue to the time of the year.

As a practical application, commercial flower growers are now able to induce plants to flower out of season by regulating the dark-light cycle. This greatly increases their business and their customers' pleasure.

Much is now known about the cellular mechanisms of photoperiodism. The length of the day (and hence of the night) is detected by a pigment, phytochrome, in leaves.

Some recent references to photoperiodism are: *Devlin (1975, ch. 20), L. T. Evans (1971, 1975), Hillman (1976), Kendrick and Frankland (1976), Leopold and Kriedemann (1975), Mitrakos and Shropshire (1972), F. B. Salisbury (1963, 1971), F. B. Salisbury and Ross (1978), H. Smith (1975), *Ting (1982, chs. 20–21), Vince-Prue (1975), and Wareing and Smith (1983).

Concluding remarks

The green plant way of life is characterized by an ability to build living substance from simple inorganic compounds; to be able to transform light into a form of energy that can be used for life processes; by having a minimal awareness of the environment, and usually a slow response to environmental cues; and, except for the green algae, being restricted to one spot.

But within these parameters the green plants have responded to the forces of variation and natural selection by evolving thousands of different species, each species having an almost unique way of life—its niche.

These sessile, mindless creatures are the transducers of energy and the synthesizers of the complex molecules essential for their own lives as well as for all heterotrophic life.

The animal way of life

Heterotrophy vs. *autotrophy*

All animals, fungi, some saprophytic and parasitic higher plants such as the Indian Pipe (*Monotropa*) and the Ground Cone (*Boschniakia*), and most microorganisms are totally dependent on organic carbon compounds produced by photosynthetic organisms and a few genera of chemosynthetic microorganisms. These dependent creatures are the heterotrophs. They require organic carbon compounds as a source of substance for their bodies and energy for their metabolism.

The contrasting way of life, autotrophy, is characteristic of the green plants and some microorganisms such as the iron and

TABLE 4. *The sources of the essential elements for organisms.*

	Green plants	Animals
Oxygen (O)	CO_2, O_2	Organisms, air, water
Carbon (C)	CO_2	Organisms
Hydrogen (H)	H_2O	Organisms, water
Nitrogen (N)	NO_3^-, NH_4^+	Organisms
Sulfur (S)	SO_4^{2-}	Organisms
Calcium (Ca)	Ca^{2+}	Organisms, water
Phosphorus (P)	$H_2PO_4^-$, HPO_4^{2-}	Organisms, water
Chlorine (Cl)	Cl^-	Organisms, water
Potassium (K)	K^+	Organisms, water
Sodium (Na)	Na^+	Organisms, water
Magnesium (Mg)	Mg^{2+}	Organisms, water
Iron (Fe)	Fe^{3+}	Organisms, water
Iodine (I)	—	Organisms, water
Silicon (Si)	?	Organisms, water
Manganese (Mn)	Mn^{2+}	Organisms, water
Copper (Cu)	Cu^{2+}	Organisms, water
Zinc (Zn)	Zn^{2+}	Organisms, water
Fluorine (F)	—	Organisms, water
Cobalt (Co)	?	Organisms, water
Nickel (Ni)	—	Organisms, water
Vanadium (V)	—	Organisms, water
Chromium (Cr)	—	Organisms, water
Molybdenum (Mo)	MoO_4^{2-}	Organisms, water
Selenium (Se)	?	Organisms, water
Arsenic (As)	—	Organisms, water
Boron (B)	$H_2BO_3^-$, HBO_3^{2-}	Not required

sulfur bacteria (*Thiobacillus, Gallionella, Beggiatoa*), the hydrogen bacteria (*Hydrogenomonas*), and the nitrifying bacteria (*Nitrosomonas, Nitrosocystis, Nitrobacter*). These organisms transduce the energy of light, or that made available by the oxidation of inorganic molecules, for their metabolism and they use carbon dioxide as a carbon source for the synthesis of organic compounds.

We might simplify matters somewhat by saying that although both heterotrophs and autotrophs must have organic compounds, the autotrophs can make their own. The substances required by green plants are no more than carbon dioxide, oxygen, water, and a few inorganic ions (Tables 1 and 4). By contrast, the animal way of life is possible only if a very large and diverse number of organic molecules are available.

In the natural world, the autotrophs take care of themselves, whereas the heterotrophs are obligate predators or parasites. Certainly a heterotroph may be a predator or parasite of another heterotroph but a cycle of heterotroph eating heterotroph cannot continue. Somewhere in the cycle a heterotroph must get back to basics and consume an autotroph.

Essential elements

We have already established that plants require a variety of elements for their growth and development. The same is true for animals. The nine elements most abundant in plants (Table 1) are among the 12 most abundant elements in animals (Table 4, where the elements are arranged in the approximate order of their abundance, by weight, in animals).

The list of elements required by animals is longer than that required for plants. At least 25 are now thought to be essential. The first five on the list account for about 95 percent of the total. The first 11 account for more than 99 percent. The classic mnemonic device, "C. HOPKINS Cafe, mighty good if taken with a grain of salt," includes the first 13 (Cafe = Ca, Fe; mighty good = Mg; Salt = Na, Cl). The remaining 12 are required in exceedingly minute amounts. Some are even toxic when present in more than trace amounts. In addition, there are data that suggest that tin and cadmium are possible additions to the list of elements essential for animals.

Some of the elements required in only trace amounts in most animals play a greater role in others. Silicon is the main component of the spicules of some sponges and the skeleton of the glass sponge. Vanadium is the essential metal in the blood of tunicates. Surprisingly, it was discovered in these lower chordates before analytical procedures had been perfected enough to detect vanadium in ocean water.

Table 4 emphasizes the very different sources for the essential elements that are required by autotrophs and heterotrophs.

Some useful references to the essential elements for animals are: Ashmead (1982), Bowen (1979), Brätter and Schramel (1980), Fowden *et al.* (1981), Frieden

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(1972), *Mertz (1981), W. J. Miller and Neathery (1977), Nickolas and Egan (1975), and *Underwood (1977).

Energy

The heterotrophic way of life requires specific organic molecules synthesized by other organisms for growth and maintenance. These same molecules also serve as a source of energy.

Correlated with this absolute dependence of heterotrophs on other forms of life, we find a myriad of ways that heterotrophs can move in seach of food or bring food to them. The terrestrial plants die where they were born; most animals can escape the bondage of immobility and go where the food is. For example, during the summer months one finds a great variety and abundance of birds in the Arctic regions. Nearly all are species that find ample food in the summer but, when the lean days of autumn arrive, migrate south. The Arctic Tern (*Sterna paradisaea*) migrates far to the south. It breeds in the Arctic but in late summer starts its long journey to the Antarctic seas where it spends the southern summer.

Sessile animals, such as sponges and many species of protozoans, coelenterates, mollusks, and ascidians, must wait for food to come to them or be able to create a current of water by means of cilia or other devices. That current of water carries food. Whereas water can be moved, earth cannot. It is not surpirsing, therefore, that there are no land animals that are sessile at all stages in their lives. Some are almost so, such as scale insects. In their immature stages they move to a source of food and there remain, fixed for life. Many internal parasites may remain in a specific site in a host yet, at some stage in the life cycle such as eggs or larvae, they must be able to get from that specific site in one host to the corresponding site of another.

There are some special habitats where the photosynthetic autotrophs cannot exist, such as caves and the sunless depths of the ocean, yet heterotrophs occur there. In caves with bats, the basic source of food is bat excrement. This is the digested residue of material from the outside world. There is often a rich assortment of heterotrophs, such as arthropods and nematodes, that depend, ultimately, on this excrement. Some caves have streams running through them that carry food materials from the autotrophic world to the obligate cave dwellers. The ultimate source of food for the heterotrophs of the abyssal zone of the ocean is the garbage that rains down from the lighted region above. In recent years a different type of autotrophy has been discovered in organisms of the hyperthermal vents of the ocean floor—chemosynthetic autotrophy (J. M. Edmond, 1983).

Other aspects of the energy requirements of organisms will be considered in the section "Interactions within Communities."

A place to live

As is the case with green plants, every species of animal has evolved as a specialist for a specific way of life, its niche, in a specific environment. Temperature and moisture are important in determining the geographic range of each species and every combination of environmental temperature and moisture has its assembly of heterotrophs. Some environments are more salubrious than others: the wet tropics show a great abundance and diversity of species; the polar regions show far less.

Considering the absolute dependence of animals on green plants, it is not surprising that the distribution and abundance of animals is often closely linked with that of specific plants. Merriam (1890) observed that some of the animals on San Francisco Peak were restricted to definite plant associations. Certainly he did not expect to find isolated polar bears or musk ox on the small arctic-like zone at the peak but he did encounter the water pipit (*Anthus spinoletta*), the main breeding area of which is Greenland, Labrador, and west across Arctic America. In the Spruce Zone he observed many species of birds and a few mammals that are typical of the Spruce Zone that extends across northern Canada. The Western Yellow Pine Zone at the lower part of the mountain had species of birds and mammals with more southern distributions.

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Within the broad geographic area of its distribution, a species will occur in a given locality only if there are spots that provide the conditions necessary for its life. The panda is dependent upon bamboo for food; the koala on a few species of eucalyptus. The yucca moth carries out its life cycle in yucca plants. Many species of insects require a specific plant species for some stage in their life cycle. As a consequence, the actual distribution of a species will be in the form of a checkerboard—occurring in patches where the requirements for life are met and being absent in the intervening areas. Buchsbaum (1948, p. 157) mentions the fascinating example of a nematode that "has never been found anywhere except on the felt mats on which Germans set their mugs of beer."

The edge of the sea provides many fine examples of restricted distributions. This is a consequence of very great environmental changes within a few vertical meters. The ocean water itself is relatively constant in chemical composition and temperature (except for the intertidal zone). The movements of the tides, however, lead to considerable variations in the zone above the low tide mark. Twice a day the water moves inland to cover an area that may be large or small, depending on the slope of the shore.

Environmental conditions are drastically different in this zone between high and low tides depending on whether the tide is in or out. When the tide is in, conditions are more uniform except for the movement of the waves. When the tide is out, the exposed shore may be blistering hot in the summer or freezing in the winter and, of course, lacks ocean water.

The intertidal zone is the most stressful environment for marine animals and plants and is populated with its specific assembly of species. Some hardy species exist in the spray zone above the average high tide level. Below that there is usually a series of narrow zones, each with its characteristic species. Connell's very interesting analysis of zonation in barnacles will be discussed in the section "Interactions among Organisms." Some general references to zonation along the shore are Allee and Schmidt (1951, pp. 237–239), E. P. Odum (1971, ch. 12), *Ricketts and Calvin (1968, ch. 14), Russell and Yonge (1936, ch. 2).

Other environmental controlling factors

The number of fascinating examples of environmental influences on animals is endless. The great synthetic ecological monographs of the last generation, Allee *et al.* (1949, sect. 2) and Andrewartha and Birch (1954, sect. 2), analyze the environment and show how each major component exerts its effect. A new synthesis by Andrewartha and Birch (1984) will be available shortly.

Rather than present first-year students with a catalog of examples (we are not discussing a course in ecology), it should be sufficient for you to give a few dramatic examples, including some that are local.

The effects of light are diverse and some of the more interesting examples are triggered by the changes of night and day. The young adults of the fruit fly, *Drosophila pseudoobscura*, emerge from their pupal cases at dawn. The gametes of the hydroid, *Pennaria tiarella*, are shed at dusk. Yet the light cycle does not exert total control; suitable temperatures are also necessary.

The moon may have its influence on human lovers but it, most assuredly, has effects on the palolo worm, *Eunice viridis*, living in the ocean near Samoa.

> All the year round it lives in holes and crevices among rocks and coral growth on the sea bottom. But true to the very day, every year the worms come to the surface of the sea in vast swarms for their wedding dance. This occurs at dawn just for two days in each of the months, October and November, the day before, and the day on which the moon is in its last quarter; the worms are most numerous on the second day, when the surface of the ocean appears covered with them .... The natives are always ready for the spawning swarms as they relish the worms as food. They catch them by dipping them up in special baskets .... The worms are eaten either cooked and wrapt up in bread-fruit leaves, or quite undressed. (Russell and Yonge, 1936, pp. 250–251)

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The palolo worm of the Atlantic spawns in a similar though less spectacular manner (Clark and Hess, 1940).

Let your students try to list the tradeoffs of the mass spawning behavior of the palolo worm during very short periods compared to spawning by individuals at different times over a long breeding season.

It is now known that many of the regularities of behavior shown by animals to the time of day or of season are controlled by "biological clocks" that, even in the absence of the environmental cue that first "set" them, continue to keep fairly accurate time. Some references to this very active field of animal cycles are: Aschoff (1965*a*, 1965*b*, 1981), Ayensu and Whitfield (1982), Beck (1960), Brady (1979), F. A. Brown, Hastings, and Palmer (1970), Bunning (1967), Cloudsley-Thompson (1961), Farner (1964), Finerty (1980), Reinberg and Smolensky (1983), Richelle and Lejeune (1980), and Saunders (1982).

A remarkable example of monitoring the environment and reacting in a highly adaptive manner is provided by a small Pacific coast fish, the grunion (*Leuresthes tenuis*). The breeding behavior of grunions is precisely adjusted to tide and time.

Each lunar month has two spring tides (above average high tides and lower than average low tides). These occur when the sun and the moon are on opposite sides of the earth (full moon) and when sun and moon are on the same side (dark of the moon, new moon). The spring tides that occur when the sun and moon are on the same side are higher than when they are in opposition.

The grunion spawns on the second, third, and fourth nights after the full moon from April through June. Males and females come ashore in huge numbers about an hour *after* the crest of the high tide and struggle up the beach as far as possible. The female actually works her body down into the sand and deposits her eggs, which the male fertilizes. Ten to 12 days later another spring tide occurs, this one higher since the moon and sun will be on the same side of the earth. This very high tide washes the eggs from the sand and the larvae hatch and are carried down to the sea.

Ask your students to suggest what might be the consequences of the grunion depositing eggs in the sand one or two hours *before* the full moon tide or during the higher spring tides that come with the new moon (it is important to remember here that the eggs reach the hatching stage in about 10 days). Your students might reach the conclusion that the grunion really knows what it is doing. For more on this fascinating story see Thompson and Thompson (1919) and Ricketts and Calvin (1968).

All aspects of the environment influence organisms to one degree or another. Some of these ways will now be listed.

Food, oxygen, and water are essential for nearly all animals. A few can live in almost completely anaerobic environments, such as the human intestine. Many desert organisms obtain their water almost entirely from metabolism, as in the basic reaction,

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$$

All, however, require food, both for cellular synthesis and energy. There is a threeway division of animals on the basis of their feeding habits: carnivores feed mainly on animals; herbivores feed mainly on plants; omnivores are catholic.

Water. Apart from being a substance required for metabolic processes, water plays a central ecological role. The major habitats of the earth's crusts are based on its presence (oceans, lakes, rivers) or nearabsence (land). Even in the watery domain, the types of aquatic habitat (salty ocean or less salty lakes, rivers, etc.) have controlling roles in the sorts of organisms that can live in each. On land, variations in the amount of water (rain forests, temperate forests, steppes, deserts) determine the organisms that can survive. In fact, the major plant associations, and therefore the types of animals, are determined mainly by the interaction of temperature and water.

Many animals have complex behaviors connected with the search for and collection of food, oxygen, and water.

Temperature. All organisms are influenced by environmental temperatures. Most ectotherms (poikilotherms) can tolerate a range of about 10 to 30°C. As a

rule, species found in more constant environments (wet tropics, the oceans, large lakes) have narrower ranges of temperature tolerance than those found in environments characterized by large temperature fluctuations. Within their temperature tolerance ranges, most species have a narrower range preferred for various activities. Temperature also influences the rate of metabolism of ectotherms. An approximate rule of thumb is that there is a doubling of the rate of metabolism for a temperature increase of 10°C.

Some ectotherms are able to maintain an almost constant body temperature by behavioral means. For example, some lizards bask in the sun to achieve a specific body temperature before they start to forage.

Birds and mammals have evolved means of overcoming the problems of fluctuating environmental temperatures by becoming endotherms (homotherms). They take on new problems: how to maintain body temperatures when the environment is cold or hot. Adjustment to cold can be solved by hair, feathers, increasing metabolism, migration, or seeking shelter. Adjustment to high temperatures can be solved by evaporation of water, devices for increasing radiation and convection of heat, insulation by hair and feathers, migration, or shelters. Some animals can avoid extreme cold by hibernation. In some cases they lower their body temperatures and, so, conserve energy. Or they may aestivate in a cooler place and avoid excessive temperatures, especially at a time of the year when food may be scarce.

Light. Sunlight is a source of energy for warming the body and making vitamin D. It makes vision possible. The relative duration of day and night, together with temperature, is important in controlling migration, breeding seasons, and changes in plumage in birds and pelage of some Arctic mammals.

Tides. The tides provide a special habitat, the intertidal zone, and twice daily flush out tide pools. Together with the light of the moon and sun, they determine the breeding season for many organisms. Ask your students how one might distinguish between the effects of tides and moonlight, since they are related, as was described for the palolo worms. Possibly they will hit upon the notion of placing the organisms in floating containers, etc.

Sound. Sound, coupled with the ability to hear, is important in communication and detection of other organisms. It permits better interactions among organisms of the same species, defines the home territory, and may help predators locate prey and help prey avoid predators. In human society sound has become one of the main features of civilization.

Wind. The movement of air has an important role in the dispersal of some organisms. Dry air, especially when moving, has an important effect on terrestrial animals: those without an effective outer covering are at risk of losing so much water that they die, as is the case of earthworms that leave their burrows during a rain and later dry out on the pavement.

Chemical substances. Chemical substances, detected by chemosensors such as organs of taste and smell, may be used to locate mates, keep a family group together, locate food, avoid predators, locate prey, or define a territory.

Other organisms. Here we have an almost infinite list of possible interrelations. In species with males and females a member of the opposite sex is required for reproduction. Even among hermaphroditic species it is not unusual for there to be an exchange of gametes between two individuals. Individuals of the same species may form family or larger groups that offer protection from predators, increase hunting success, and increase the chance for survival of offspring. In some species (social insects, ourselves) a complex society has evolved that allows a division of labor. Interrelations with other species include being predator or prey, host or parasite, as well as associations for mutual benefit.

For general treatments of how the components of the environment influence organisms see Allee *et al.* (1949), Andrewartha and Birch (1954, 1984), Krebs (1978), E. P. Odum (1971), Ricklefs (1979), and R. L. Smith (1966). For the physiolog-

ical aspects see Gordon (1982), R. W. Hill (1976), Hoar (1983), Prosser (1973), and Schmidt-Nielsen (1983).

Concluding remarks

Some of the current hypotheses for the origin of life hold that the first self-replicating "things" did so in an environment rich in organic molecules—swimming in their food, so to speak. It could hardly have been otherwise: there are no known scientific processes that could have formed an autotroph in a single step. Thus, a reasonable hypothesis is that the first forms of life were molecular heterotrophs.

The animal way of life is characterized by a dependence on autotrophic organisms, mainly green plants, for complex organic compounds. In addition there is a requirement for oxygen (usually) and somewhat more than a dozen mineral elements that can be satisfied from inorganic sources. Since the animal way of life is dependent on organic food, it is not surprising that special behavioral mechanisms have evolved that enable the animal to obtain that food: either the animal can move in search of food or, if sessile, has mechanisms to move the food toward it. The ability to obtain food almost always requires a nervous system and special sense organs. Animals usually must be active if they are to live.

Thus the animal way of life is that of dependent, motile, sentient organisms or, we might say, of active, brainy, parasites.

Interaction among organisms

If the first self-replicating "things" in that hypothetical primal sea had possessed an error-proof system of replication, they would have ceased to exist when their substrates had been consumed. But self-replication today, and presumably in the past, is subject to error. These errors are mutations, which are the basis of evolutionary change and, hence, the basis of the species' ability to adjust more closely with its environment.

Errors in the replication of the genetic code are the basis of the organic diversity that has been a feature of life through the ages. To this propensity for error we must add that, unless restrained in some manner, organisms continue to replicate until the supply of materials they require has been exhausted.

Competitive exclusion

The twin forces of genetic variation and the capacity of organisms to increase their population size insure that Darwinian Natural Selection will permit survival of organisms that have evolved a new way of living, that is, have evolved a new niche. A way of life requires three main components: a suitable place to live, including the climate and other organisms; a suitable source of chemical substances (food); and a usable source of energy (food, light).

It appears that every species of organism has its unique niche. To be sure, there may be considerable overlap of niches, especially of closely related species. But the argument is that if two species had *exactly* the same way of life, one of them must be slightly better than the other and so over time would out-breed, out-fight, or out-eat the other and so prevail.

Time and time again, when it has appeared that two species have identical niches, careful analysis has shown this not to be so (E. P. Odum, 1971, pp. 213–220). One of the famous cases is that given by Lack (1945) who studied two species of cormorant in England. The two are so much alike that it takes an experienced ornithologist to distinguish them in the field. "Both species nest on cliffs overlooking the sea, and both feed by swimming under the water for fish." On those same cliffs, however, *Phalacrocorax carbo* prefers to nest on flat ledges and *P. aristotelis* in holes or under rocks. The feeding habits are markedly different. *P. carbo* feeds in harbors and estuaries and the main food is flatfish, prawns, and shrimp. *P. aristotelis* feeds out at sea; its main food is sand eels. Thus the two species partition the environment for their breeding sites, the places where they search for food, and the food they eat. Thus the possibility of competition between them is greatly reduced.

Many studies of pairs of species that

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appear to have identical niches have revealed that they do not. The working hypothesis of most ecologists is, therefore, that "no two species can occupy identical niches." This is commonly known as "Gause's Principle" but as Hardin (1960) points out, the idea precedes Gause and was never expressed by him. Hardin prefers the term "competitive exclusion principle" meaning that "complete competitors cannot exist" (but see Gause, 1934*a*, 1934*b*, and 1936).

The competitive exclusion principle is so completely accepted, that if a study reveals two species appearing to occupy the same niche it is suspected that the study is incomplete and that further investigations will uncover differences in habitat, behavior, or food. However, it is assumed that two species can coexist if there is as much as a slight divergence between their niches.

Nevertheless, it must be admitted that differences sufficient to permit coexistence often seem trivial from a human perspective. Those two species of cormorant may feed on different fish in different localities but they are, after all, both fish-eating heterotrophs. The flatfish eaten by *P. carbo* and the sand eels eaten by *P. aristotelis* both end up as the same end products of digestion: amino acids, fatty acids, glycerol, etc.

Cycles of substance

One may ask the question, therefore, how it is possible for the heterotrophic way of life to have existed for at least three billion years, demanding as it does a large and diverse source of molecules? Surely in that long period the supply of substances would have been exhausted. There are three closely related answers: individual death, biospheric cycling, and the evolution of a variety of niches in which the waste products of one way of life are the resources of another.

Somatic death returns to the environment the substances that the organism acquired during life. An organism does no more than borrow molecules from the environment, rearrange them for its own use, and finally return them to the storehouse of the earth's crust (Genesis III, 19 and Ecclesiastes III, 20 put it much better).

Philosophers, theologians, and lesser mortals have long speculated on the meaning of death. It would be interesting to ask your students for their thoughts on this matter. Their answers should provide a good opportunity to contrast different kinds of explanations: philosophical, religious, poetic, scientific. The biologists' explanation is that those species with sexual reproduction and individual death have, in the long run, proved to be more successful. This success is due presumably to the genetic recombination that occurs in sexual reproduction. This provides a huge array of genotypes that have allowed evolution to perfect organisms for every conceivable niche. Death removes some organisms to make room for the new experiments in living.

The cycles of substance and energy in which the many different ways of life complement and supplement one another in ways that result in a near constancy of life and non-life on the surface of the earth will now be discussed.

Chemical cycles: C, H, O. The internal metabolic reactions of autotrophs and heterotrophs are not the concern of ecology but what goes in and what comes out is much of what ecology is all about. The many reactions involved in the production of carbohydrate, such as glucose, by green plants in light and its complete utilization by plants in the dark and by animals can be reduced to these simple equations:

Green plants in light—

$$6CO_2 + 6H_2O + \text{energy} \rightarrow C_6H_{12}O_6 + 6O_2$$

Plants in darkness and animals—

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6H_2O + 6CO_2 + \text{energy}$$

The energy made available is 686 kilocalories per mole of glucose.

Thus for the production of carbohydrate by plants and its utilization by animals, the chemical substances that enter and leave are balanced. Similar reactions apply to fats and other nutrients.

For the cycles of carbon, oxygen, and hydrogen see Bolin (1970), Botkin (1977), Buswell and Rodenbush (1956), Cloud and Gibor (1970), C. S. Fox (1952), Penman

(1970), U.S. National Commission for the International Biological Program (1975), and Woodwell and Pecan (1973).

Chemical cycles: nitrogen. The story for proteins, nucleic acids, and those molecules composed of other than C, H, and O is more complex. Nitrogen leaves the bodies of living animals as part of the waste product molecules of urea, uric acid, and ammonia. When animals and plants die their nitrogen is present as parts of their molecules of protein, nucleic acid, etc. All of these nitrogen compounds are valuable substances to some kind of scavangers, mainly microorganisms. They use the compounds for energy and synthesis, and eventually convert them to ammonia (NH_3) or ammonium ions (NH_4^+). Both of these nitrogen molecules can be taken up by the roots of green plants and used for the synthesis of proteins etc.

Both NH_3 and NH_4^+ still contain energy and some genera of soil bacteria are able to use these molecules in their chemosynthetic lives. *Nitrosomonas* converts them to nitrite (NO_2^-) in reactions that produce 65 kilocalories per mole of ammonia. *Nitrobacteria* is able to squeeze out another 17 kilocalories when it converts nitrite (NO_2^-) to nitrate (NO_3^-). Green plants use nitrate as the preferred source of nitrogen. Nitrite is highly toxic to plants.

The nitrogen cycle is made more complicated by one group of microorganisms that converts the more complex nitrogen molecules to nitrogen gas, the denitrifying bacteria, and another group that converts nitrogen gas to complex nitrogen molecules, the nitrogen-fixing bacteria.

Pseudomonas denitrificans is one of the denitrifying bacteria that can extract large amounts of energy by converting nitrite and nitrate to elemental nitrogen. This seemingly counterproductive activity is, in fact, a vital part of the whole mechanism that keeps nitrogen available for green plants, and so indirectly for all of us dependent heterotrophs (Delwiche, 1970).

In contrast are the nitrogen-fixing bacteria, such as *Rhizobium, Azotobacter, Klebsiella,* and *Spirillum,* which use atmospheric nitrogen for synthesizing complex organic molecules.

Since the breakdown of nitrogen compounds to free nitrogen releases large amounts of energy, it will be necessary that an equal amount of energy be available to *Rhizobium* and other nitrogen fixing organisms if they are to use nitrogen for the synthesis of organic compounds. The energy is obtained in a fundamentally important manner from a host plant with which *Rhizobium* becomes associated.

Rhizobium invades and forms nodules on the roots of various species of legumes such as beans, peas, clover, and alfalfa. In these nodules the *Rhizobium* produces an enzyme, nitrogenase, which catalyzes the conversion of nitrogen gas to ammonia, a form that can be used by both the bacterium and the host plant. The legume, in a real sense, has a resident nitrogen fertilizer factory in its nodules. The nodules also contain a hemoglobin-like compound known as leghemoglobin that is able to bind oxygen and protect nitrogenase, which is sensitive to oxygen. The host and symbiont appear to cooperate in forming this molecule; the globulin part of the leghemoglobin is produced by the legume and the heme by *Rhizobium.*

Two of the micronutrients, molybdenum and cobalt, are essential for the *Rhizobium*-legume cooperative effort. Molybdenum is part of the nitrogenase molecule.

The association of *Rhizobium* with a legume is an example of symbiosis, the close association of two different species—in this case for mutual benefit. The host plant provides *Rhizobium* with energy, a source of molecules, and a place to live. The *Rhizobium* in turn provides the host plant with a substance often in short supply—nitrogen in a usable form.

Long before the legume-*Rhizobium* relationship was discovered, observant farmers had found that, whereas most crops decrease the fertility of soil, clover and other legumes actually increase it. It therefore became common practice to rotate crops by sowing wheat or other crops for several years and then planting legumes for one year.

The lightning of an electrical storm can also convert atmospheric nitrogen to ammonia and other molecules. This pro-

cess accounts for about four percent of the nitrogen fixed naturally (Ehrlich, Ehrlich, and Holdren, 1977, p. 76).

For information on the nitrogen cycle see M. Alexander (1984), Burns and Hardy (1975), Burris (1978), Delwiche (1970), H. J. Evans (1956), Henry (1966), Hubbell (1981), Minchen and Pate (1973), Nutman (1976), Quispel (1974), Stewart (1966, 1967), Stewart and Rosswall (1982), Streicher and Valentine (1973), and U.S. National Committee for IUBS (1969).

Chemical cycles: micronutrients. The other elements necessary for living organisms also cycle between the living and non-living sectors of the environment. When organisms die the sulfur and phosphorus, so necessary for proteins and some other cellular molecules, pass to the bodies of the organisms of decay. In time they are liberated in the soil where they are absorbed by plants and rebuilt into organic compounds. Animals obtain these elements mainly from plants and to a limited degree as inorganic molecules dissolved in water.

Some references to cycles other than carbon, oxygen, hydrogen, and nitrogen are Bormann and Likens (1967), Deevey (1970), Duvigneaud and Denaeyer-de Smet (1975), Garrells, Mackenzie, and Hunt (1975), Higinbotham (1973), Kellogg *et al.* (1972), MacIntyre (1970), Missouri Botanical Garden (1975), and Reichle (1975).

For general discussions of the cycles of substance the following, or any textbook of ecology, can be consulted. Barbour, Burk, and Pitts (1970, chs. 11–12), Deevey (1970), *Ehrlich, Ehrlich, and Holdren (1977, chs. 2–3), Garrels, Mackenzie, and Hunt (1975), Hutchinson (1970), Institute of Ecology (1972), Lieth and Whittaker (1975), B. Mason (1966), *E. P. Odum (1971, ch. 4; 1975, ch. 4), Ricklefs (1979), ch. 42), U.S. National Committee for the International Biological Program (1975), and Whittaker (1975, chs. 5–6).

The flow of energy to a sink of heat

In the interactions that occur among the major trophic groups of organisms, none impose greater restraints than the Second Law of Thermodynamics. When energy flows from one physical system to another, or from one species to another, some is always lost as heat. The remainder can do mechanical, chemical, or other sorts of work. All of the energy captured by photosynthesis eventually returns to the environment as heat but, before it does, a slight fraction will have been devoted to the work of living.

Were the earth a closed system thermodynamically, that is with no energy entering or leaving, its complex molecular structures—mainly those associated with life—would slowly break down to very simple chemical substances. Life would end. But the earth is an open system and the constant inflow of energy from the sun permits the synthesis and maintenance of complex molecules.

Organisms must obey the same laws of nature that apply to other assemblages of matter, so the manner in which the Second Law impinges on life can be illustrated by a mechanical analogy. When fuel is burned in a steam engine that will perform mechanical work only about 30 percent of the energy in the fuel is converted to mechanical energy. The rest is lost as heat.

You may wish to have your students consider a theoretical Rube Goldberg contrivance using fossil fuel to power a steam engine that will run a generator, which will produce electricity, which will heat water, which as steam will power a second steam engine, etc., etc. They will soon discover how rapidly the system loses the ability to do useful work. This is not a consequence of inept engineers but the inability of energy to be moved from one machine to another without a fraction, and often a large fraction, of the energy being converted to heat. For most purposes the heat will be a waste product.

The efficiency of a modern automobile gasoline engine is about 30 percent. The final efficiency when the engine gets all those gears and wheels moving is about 15 percent. If we consider the energy required to obtain crude oil, refine the oil, and transport it, only about five percent of the energy in the crude oil is used to move the automobile along the highway (E. Cook, 1976).

The same principles apply when one organism consumes another, but for the

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most part organisms are less efficient. We saw earlier that green plants utilize only one percent or less of the light energy that reaches them. They are the lowest trophic level, that of producers. The herbivores that feed on the plants are the next higher trophic level, that of the primary consumers. The carnivores that feed on the herbivores are secondary consumers. And the secondary consumers might be consumed by tertiary consumers, and so on.

One of the most important restraints for all consumers is that, as food energy moves from one trophic level to another, only about 10 to 20 percent will be used to produce the organisms of the next higher trophic level. As Ehrlich, Ehrlich, and Holdren (1977, p. 131) put it, "it might take roughly 10,000 pounds of grain to produce 1,000 pounds of cattle, which in turn could be used to produce 100 pounds of human beings." That is a sobering fact.

Schaller (1972, p. 460) quotes H. Hendrichs' estimates for the numbers of mammalian herbivores and carnivores in the Serengeti National Park of Tanzania. There were 1,740,500 individuals of 12 prey species (zebra, giraffe, buffalo, and gnu) compared with 28,250 individuals of predators (lion, leopard, cheetah, and four canines). Thus there were 62 prey individuals for each predator. Since the prey species average larger than the predator species, the differences in biomass is even greater. We might estimate 100 kilograms of prey for each kilogram of predator. These differences reflect the Second Law constraints on the transfer of energy between species of different trophic levels.

Your students might be asked, on the basis of this information, what should be the policy for the Minister of Agriculture of a Third World country with limited capabilites for producing food and a deficit trade balance.

See Ehrlich, Ehrlich, and Holdren (1977, pp. 128–135), Gates (1971, 1980), Gosz, Holmes, and Likens (1978), Lindeman (1942—the seminal paper), E. P. Odum (1971, ch. 3; 1975, ch. 3), Oort (1970), Pimm (1982), Putnam and Wratten (1984, ch. 3), Ricklefs (1979, ch. 41), *Whittaker (1975, ch. 5), and *Woodwell (1970).

The cyclic balance of substance and the flow of energy in the biosphere are natural phenomena of intricate beauty. They are both prerequisite to and expressed in patterns of life. With apologies to John Donne we must say that, even for the autotrophs, "no species is an island, entire of it self."

There are innumerable types of interaction among organisms. We will consider several examples.

Mycorrhizae

One of the most important of all interrelations between different sorts of organisms has remained unemphasized and unappreciated until recently. It is the symbiotic relationship between various species of fungi and virtually all gymnosperms and angiosperms that results in the formation of mycorrhizae. The word means "fungus root." It is becoming increasingly evident that mycorrhizae are necessary for the life of nearly all species of higher plants.

The discovery of the importance of mycorrhizae for plant growth has many features in common with the discovery of the essential micronutrients. In both cases something goes wrong in an experiment and it becomes important to learn why. In science when something "goes wrong" it often means that the experiment one believes is being performed is not—by oversight or by accident a slightly different experiment is underway. More often than not a bungled experiment provides no useful information; yet sometimes it does—as was the case when Alexander Fleming discovered the antibiotic action of *Penicillium* when that mold appeared as an accidental contaminant in some cultures of *Staphylococcus*.

Consider the following case of something that went wrong (Vozzo and Hacskaylo, 1971; Hacskaylo, 1972). At least as early as the 1920s, efforts were made to grow pine trees in Puerto Rico. Many species were tried and even some hybrids, in the belief that they would be more hardy. Germination was splendid but after the seedlings reached a height of a few inches they became chlorotic—a sign that the plants were not getting enough minerals. The syndrome suggested, most strongly,

that the problem was lack of phosphorus. This in itself was surprising because pines are known to be able to flourish on land poor in essential minerals.

Nevertheless, the problem should have been easy to solve—add superphosphate fertilizer. That was done but to no avail; the seedlings never grew more than a sickly few inches and usually had but a few needles at the tip of their stick-like trunks.

During those years, reports were appearing about the fungi that invaded the roots of some trees, including pines, and produced a mat-like growth that surrounded the roots and invaded the roots themselves—the root and fungus together being the mycorrhiza. Since most fungi produce a disease when they invade plants, it was assumed at first that the mycorrhizae must be pathological growths. But as more and more observations were made, there was clear evidence that mycorrhizae were "good." The hypothesis was developed that somehow they helped the pine trees growing in soils deficient in nutrients.

Would mycorrhizae help those chlorotic pine seedlings in Puerto Rico? A crude first experiment might be to mix some soil from a place were the pine trees grew normally with the soil in the Puerto Rico nursery. Such soil was obtained from under mature pine trees growing near Bent Creek, North Carolina and shipped to Puerto Rico.

The experimental plants consisted of 64 scrawny seedlings that were one year old. Soil from North Carolina was added to the soil of half of the seedlings. The other seedlings were kept as controls. One year later the roots of the plants that received the North Carolina soil were found to be covered with mycorrhizae and the largest pine was 1.5 meters in height. Most of the controls were dead. In another experiment lasting three years pine seedlings without mycorrhizae grew no more than one foot and had few needles whereas those with mycorrhizae reached eight feet and were fully-needled trees.

By the 1970s it was known that the importance of mycorrhizae extended far beyond pines and other conifers growing on poor soil. It appeared that they might be essential for virtually all higher plants.

There are no species of mycorrhizae. Mycorrhizae are structures formed by associations of fungi and the host plants. Some of the common genera of the fungal portion of the symbiont are *Russula, Tuber, Amanita, Suillus,* and *Rhizopogon.* If some of those generic names sound familiar, they should. They are of some of the famous and infamous mushrooms. *Tuber* includes the truffles—the gourmet's delight. Both the Death Cap and the Destroying Angel belong to the genus *Amanita* and their common names suggest what they do. These fungi consist of an extensive network, the mycelium, that permeates the soil and forms mycorrhizal growths on the root of specific kinds of plants. At certain seasons of the year the mycelium sends up fruiting bodies and these are "mushrooms."

There is a lot going on in soil that we never see. One of the more dramatic experiments showing the role of the mycorrhizal fungi was done by Björkman (1960). He introduced radioactive phosphate and carbon into spruce trees and found that the tagged molecules appeared in some *Monotropa* (Indian pipes) growing under the trees. Björkman concluded that the radioactive molecules had moved from the spruce trees through the mycorrhizae to the *Monotropa.*

The mycorrhizae are divided into three main groups.

1. In the ectomycorrhizae the hyphae of the fungus extend among the root cells of the host plant but do not enter them. Spores of the fungus are widely distributed in the soil and are stimulated to germinate by special secretions of the host-to-be. They secrete an enzyme that aids in penetrating the root. The ingrowth of the fungal hyphae alters the morphology of the root. For example, the root hairs are much reduced as the hyphae begin to assume their function. The fungi involved in this group are those with fruiting bodies above ground—the mushrooms. The mushrooms do not form unless the fungus makes contact with an appropriate species of host plant. Some of the hosts involved are pine, oak, beech, walnut, and hickory. The ectomycorrhizal fungi are absent from large

areas of the world. That was the problem in Puerto Rico, as it is in Australia where similar problems were encountered in establishing pine tree farms.

2. The endomycorrhizae, unlike the ectomycorrhizae, produce spores underground and, as their name implies, the hyphae of the fungus actually enter the root cells. Most of the symbiotic associations are of this type. Nearly all of the angiosperms, including our agricultural plants (all cereals, legumes, fruit trees, tomatoes, cotton, etc.) have mycorrhizae of this sort, as do many of the conifers.

3. The ectendomycorrhizae send their hyphae between, as well as into, root cells. They are rare and their role is not well understood.

This association of fungus and green plant is a symbiotic interaction of a heterotroph with an autotroph. The green plant supplies food to the fungus. The mycelium of the fungus ramifies through the soil and assists the plant in obtaining phosphate and other salts, and indirectly influences water uptake and synthesis of plant growth hormones. According to Moore-Landecker (1982, p. 496) "Probably all soils but the most fertile agricultural soils are somewhat deficient in nutrients, which makes ectomycorrhizal formation obligate for most plants in woodlands." The fungus extends the plant's root system and even connects plants with one another to allow exchanges of materials (the spruce—*Monotropa* experiment). The mycorrhizal mat on the roots seems also to prevent some pathogens from entering.

This extraordinary symbiosis is not only critical for the participants but, quite literally, is essential for the life of terrestrial heterotrophs as well. It is hard for a phenomenon to be more important than that.

Useful references are Björkman (1960), Cooke (1979), Gianinazzi-Pearson and Gianinazzi (1981), *Hacskaylo (1972), Harley (1960, 1968), Harley and Russell (1979), Harley and Smith (1983), Lincoff (1981), Lindeberg (1981), Mallach, Pirozynski, and Raven (1980), Moore-Landecker (1982, pp. 493–501), Rayner (1927), *Ruehle and Mark (1979), St. John and Coleman (1983), Sanders, Mosse, and Tinker (1975), Went and Stark (1968), and Wilde (1968).

Symbiosis of reef corals and algae

The tropical seas are usually a nutrient-poor environment with the main deficiencies being usable phosphate and nitrogen. In part this is a consequence of the fact that supplies of these substances are mainly in the bodies of organisms and, when the substances are released by death and decay, they are rapidly consumed by the phytoplankton, which in turn are consumed by zooplankton, which in turn are consumed by larger heterotrophs.

Species tend to increase in population size unless checked in some manner. In the warm tropical seas with year-round light, organisms remain active—there is no winter to induce dormancy or death. Life appears to expand to the limit set by resource availability—to be always on the verge of starvation. In the nutrient-deficient tropical seas, evolutionary pressures have promoted the symbiotic associations of heterotrophs with autotrophs. The combination can carry out an internal cycling of many of the essential molecules.

One of the most spectacular of these symbiotic associations is that of reef corals and dinoflagellates (green algae) of the genus *Gymnodinium*. In fact, together they are responsible for the most stupendous of all productions of life—the coral reefs. A climax is reached with the Great Barrier Reef, which extends for more than 2,000 kilometers (1,200 miles) along the east coast of Australia. It is said to be the only product of living organisms that can be seen from outer space. No human monuments or cities are visible from so far away.

The dinoflagellate invades a coral polyp and becomes situated in the endoderm. There it carries on photosynthesis. It supplies itself and, to a considerable degree, the polyp with organic molecules and during the day with oxygen. The coral polyp contributes carbon dioxide, nitrogen wastes, and a place for the alga to live. Salts and water pass through the cells of the polyp to the alga. The polyps, although sessile, can move their tentacles and with these can capture zooplankton, which con-

tribute to the supply of nitrogen compounds required by both polyps and dinoflagellates.

Many of the details of this symbiotic association are still unknown but its long duration (the association of coral and algae goes back at least to the Triassic and possibly to the Ordovician) and the fact that it is so productive suggests that the algal-coral combination is a more efficient way of living than is either life alone.

It would be interesting to have your class predict what might be the yearly cycle of abundance for phytoplankton and zooplankton in the oceans at high latitudes where the amount of light available in the winter months is insufficient for more than minimal growth of phytoplankton. See Russell and Yonge (1936, pp. 243–250) or, for the same phenomenon in large northern lakes, E. P. Odum (1971, p. 307–308).

The literature may be approached with Muscatine (1973), Muscatine and Porter (1977), D. L. Taylor (1983), Trench (1979), and Yonge (1930, 1958, 1968).

There are similar symbiotic associations between the giant clam *Tridacna* and the alga *Symbiodinium* and between an alga and the marine flatworm *Convoluta*.

Lichens

Another symbiotic association that has been most successful in a difficult environment is that of the lichens, which is a combination of fungus and algal cells. Lichens are usually found where other plants cannot grow, such as on the trunks of trees, on bare rocks, and in the almost lifeless regions of high mountains. Most of Antarctica's plant species are lichens. About 20,000 species have been described worldwide but the whole question of "what is a species?" in lichens is made difficult because two very different organisms are involved. Thus a species of alga and a species of fungus combine to make a species of lichen!

The lichen is successful in allowing life in a habitat that is not acceptable for either alga or fungus alone. This is one more example of the pressures of evolution tending to develop some form of life that can occupy every conceivable habitat. Lichens play an important role for other plants. Once they are established on a bare rock, soil may accumulate near them. In time, the site becomes suitable for other types of plants such as mosses, which overgrow and kill the lichens.

Although the fungus-algal association is usually cited as a mutually advantageous arrangement, the fungus seems to make the lesser contribution. To be sure it supplies a place to live for the alga. The food of the fungus, including vitamins, is provided by the alga. Thus, it seems to some that the fungus should be regarded as a parasite. Ahmadjian and Jacobs (1983) write "It seems paradoxical that a parasitic relationship can be so successful. A lichen is an example of two different organisms, alga and fungus, that have evolved a successful strategy for survival."

This raises an interesting scientific point. The very fact that the lichen finds a place to live that is generally impossible for either of its component species suggests that the association is effective and that future studies will provide more evidence of mutual cooperation rather than parasitism.

For further information see Ahmadjian (1967, 1982), Ahmadjian and Hale (1973), Ahmadjian and Jacobs (1983), Hale (1974), Moore-Landecker (1982, pp. 484–492), Seward (1977), and A. L. Smith (1975). For additional examples of symbiosis of algae with other organisms see Goff (1983).

Tolerant as they are of harsh conditions, lichens have not adapted to the modern technological world. They are so susceptible to sulfur dioxide and hydrogen fluoride that they can be used as a very sensitive test for air pollution. See Ferry *et al.* (1973) and Hawksworth and Rose (1976). Showman (1975) recorded the elimination of lichens near a coal-fired generating plant and later (1981) studied the recolonization after the pollution levels were lowered. If your university is in an urban setting, it would be interesting for your students to see how far they must go from the campus to find natural areas where the rocks have good growths of lichens. Don't check the roadsides only—automobiles pollute also!

Molybedenum and clover; copper and sheep

Begin to study any problem in ecology and soon much of biology will be involved and with ever increasing frequency human problems must be considered.

Australia is not the best of lands for agri-

culture. Farming is restricted to localities along the coasts and the major river valleys. Much of the vast interior has so little rainfall that it is not suitable ranch land ("stations" in Australia) for sheep and other grazing animals. In many localities the soil is deficient in nitrogen, phosphate, sulfur, and other nutrients. The native plants have evolved for survival under these harsh conditions.

The study now to be described involved unimproved pasture land in South Australia where the soil is deficient mainly in nitrogen, phosphate, and sulfur. The native plants provide poor forage for sheep, the desired product, so efforts were made to introduce domesticated plants that would provide a better food supply. Subterranean clover (*Trifolium subterraneum*) is one such plant. This species of clover grows better than others in areas characterized by acid soils, rainfall over 40 cm per year, and hot dry summers. It was thought that, since it is a legume, it should be able to cope with the nitrogen deficiency. Phosphate fertilizer could be added to supply the other main deficiency.

The fertilizer was made from phosphate rock obtained from an island north of Australia and treated with sulfuric acid to produce superphosphate of lime fertilizer. This fertilizer would supply the phosphorus and the sulfur; *Rhizobium* in the clover's nodules should supply the nitrogen. A good source of nutrition should have been available for the sheep.

But the clover did poorly. Some farmers made the chance observation that clover grew much better where eucalyptus trees had been burned. The wood ashes seemed to contain a "growth factor."

At this stage of the analysis World War II broke out and the military forces of Japan overran the island where the phosphate rock was being mined. The great importance of food for the Allied war effort made it imperative that the production of mutton continue so alternate sources for phosphate rock were sought. South Africa had phosphate mines and, since the Allied naval forces controlled the Indian Ocean, this was a feasible source for Australia.

The African phosphate proved to be different. Curiously, it did not have to be supplemented with wood ashes. This problem was studied by A. J. Anderson and by 1942 he had the beginnings of the answer. It turned out that the South Australian soil was deficient in molybdenum. The wood ashes contained small amounts of this element as did the phosphate rock from Africa. The phosphate rock from the now captured island did not (Anderson, 1942). Phosphate rock is not, of course a pure chemical substance. Molybdenum just happened to be present in one sample and not in the other.

Many additional studies showed that the amount of molybdenum required for vigorous growth of subterranean clover is exceedingly small—five grams per hectare or less than half a teaspoon per acre. Once it had been discovered that molybdenum was deficient in some soils, an extensive survey was made of other soils that produced poor crops or forage. It was found that millions of hectares in Australia are deficient and that they could be "cured" by adding traces of molybdenum salts.

The economic importance of this discovery was enormous. Stout (1972) provides an interesting analysis. When the fields were cleared of native plants (which were nearly worthless for forage), fertilized with the superphosphate made from the molybdenum-deficient phosphate rock, and then planted with clover, each sheep required 1.6 hectares (four acres) for grazing. When molybdenum was added, the growth of the clover was so much greater that a hectare could support from seven to ten sheep—a twelve- to sixteen-fold improvement.

Stout then compares the relative amount of additional energy produced by adding molybdenum to the soil to that produced by an atomic bomb. In the state of Victoria alone between 2 and 3.2 million hectares of grazing land had been treated and made suitable for the growth of the clover. There alone each year's production of clover would have the energy equivalent of 1,400 to 2,300 A-bombs.

Many more questions remained. Why did not the native plants show signs of molybdenum deficiency? The answer proved to be complex. Recall that the soil was deficient also in nitrogen, sulfur, and phosphorus. If, in an effort to improve the pasture, fertilizer with these elements but not

molybdenum was added, the native plants grew more vigorously but *then* began to show signs of mineral deficiency. Why?

This would be a good place to have your students suggest hypotheses and experiments. They might be able to provide a satisfactory hypothesis but, even if they cannot, they will have done some original thinking about the problem. Molybdenum is essential for all plants, so it is not a matter of the native flora being able to live without this element. Under natural conditions there are only a few plants per unit area and these absorbed the traces of molybdenum present, which is enough to allow minimal growth. In time the plants die and the molybdenum is recycled to other plants. The soils are deficient in other elements as well. Thus when phosphorus and sulfur were added as superphosphate, the native plants increased in number and size and soon the point was reached where molybdenum became a limiting element.

For any organism there will be numerous substances and conditions necessary for life. Any one of them may be absent or inadequate and then appear to be *the* single controlling factor. This concept was first clearly expressed by Liebig (1840; or so it is said; I cannot find such a statement in the American edition of 1841) and for that reason is known as "Liebig's Law of the Minimum." Liebig was speaking of chemical substances of importance to agricultural plants. Later Blackman (1905) extended it to all conditions. W. P. Taylor (1934) restated the concept as "The growth and functioning of an organism is dependent on the amount of the essential environmental factor presented to it in minimal quantities during the most critical season of the year, or during the most critical year or years of a climatic cycle." See also E. P. Odum (1971, ch. 5).

Your students should also be able to account for the fact that molybdenum deficiency becomes more severe when the land, whether covered with native plants or clover, is grazed by sheep. Molybdenum is also an essential element for sheep (Table 4) and when the sheep went to market so did the traces of molybdenum locked in some of their enzymes.

What does the molybdenum contribute to the clover? Subterranean clover is a legume and its nodules contain the nitrogen-fixing bacterium, *Rhizobium*. Recall also that its important enzyme, nitrogenase, contains molybdenum.

See if your students can account for these results:

1. The clover grows well when superphosphate and molybdenum are provided.
2. When provided with superphosphate alone, growth is very poor.
3. When provided with superphosphate and nitrate, but no molybdenum, growth is fine. Suddenly molybdenum seems not to be required!

If a hypothesis is slow in coming, provide these additional data.

4. The nodules on the clover in Experiment 1 are well developed.
5. There are few or no nodules on the clover in Experiments 2 and 3.

These data may lead your students to suggest this hypothesis. Molybdenum is required in very small amounts by the clover. More is required if the nodules are to develop and contain normal amounts of nitrogenase. When the nodules are normal, they will supply the clover with nitrogen. The soil probably contains enough molybdenum to permit minimal growth of the clover alone but not for the development of normal nodules (Experiments 2 and 3). Thus in Experiment 3 growth was about normal because the additional nitrogen was compensating for what would have been produced had the nodules been normal.

But the purpose of those pastures in Australia is not to grow clover but to grow sheep. And sheep have their problems also. When they graze on land deficient in molybdenum they become ill and eventually die. Molybdenum is essential for animals as well (Table 4) where it is part of xanthine dehydrogenase and other essential enzymes. The problem for the sheep is not merely a molybdenum deficiency. When their forage contains insufficient molybdenum, they accumulate copper in

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their livers, develop chronic copper poisoning, and eventually die (Underwood, 1977, ch. 4 and pp. 96–99).

It is now known that the United States also has problems with molybdenum availability. The acid sandy soils of the coastal strip of the southeastern states may be deficient. Other soils in California, Oregon, and Florida have excess concentrations that are toxic to cattle, which are the least tolerant to molybdenum excess and deficiency of any domestic animal.

See A. J. Anderson (1942, 1946, 1956*a*, 1956*b*), Cunningham (1955), Dick (1956), H. J. Evans (1956), Mortvedt *et al.* (1972), and Rubins (1956).

Competition

When individuals living together in the same locality seek a resource that is insufficient for all, they are said to compete with one another. Competition may be intraspecific, that is, among individuals of the same species; or interspecific, that is, among individuals of two or more species.

The concept of competition occupies an important place in biological theory. It is essential for Darwinian evolution: the genetically more fit are able to gain a greater share of the insufficient resources and have a better chance for successful reproduction. This notion of the survival of the fittest was often imagined by Victorians as a widespread and gruesome business. It was "Nature, red in tooth and claw" to quote Alfred, Lord Tennyson (*In Memoriam* lvi).

Darwin knew better. A lion killing an antelope on the Plains of East Africa was red in tooth and claw, but in most places and at most times one does not observe bloody competition among the more conspicuous animals. In fact, one must look carefully to find evidence of competition. As we have seen earlier, in the case of Lack's cormorants the two species are kept from intensive competition because they have different ways of life. The evolution of specific niches, then, has the effect of reducing competition. The intensity of interspecific competition will depend upon the degree of overlap of the niches of the putative competitors and the availability of common resources.

The situation is different for individuals of the same species living in the same locality. The niches of the different individuals will be essentially the same. There may be devices which reduce competition, such as regulation of population size or the formation of territories. Thus, during the nesting season some species of birds establish territories that provide adequate food supplies. They defend these territories mainly by bluster and bluff and drive away intruders, they do not annihilate them. Then again, population size may be kept so low by severe climatic conditions or predation that resources remain adequate for all.

You may wish to ask your students to consider the degree to which intraspecific competition occurs in the human population and, if it does, what forms it takes.

It is most unusual for all of the offspring in any generation to survive. An oak tree in a forest may shed a thousand acorns yet few, if any, will survive to become mature trees. This is not a consequence of their being genetically less fit but solely because all places to live have been preempted. A chance for life will come only if one of the existing mature trees dies from disease or natural causes or is destroyed by wind, fire, drought or other episodic events. In the real world it is more often the survival of the luckiest rather than the survival of the fittest. Yet evolutionary change depends on that small fraction of situations where those that survive are superior in some way to those which do not.

Types of interspecific interaction. Remembering that the long term consequence of evolution is the increase in the number of niches (ways of life) it is not surprising that innumerable types of interaction between the various niches will have developed. Some of the main types will be listed, and throughout this essay examples of many others have been and will be provided.

A lichen and a tree on which it grows influence one another hardly at all. The tree provides a place for the lichen to live but the survival of the tree is not influenced by the presence of the lichen.

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A cattle egret feeding on the back of cattle or Cape Buffalo is obtaining food and relieving its host of ticks. Both benefit. In a tick-buffalo relation, the tick obtains a blood meal and the host loses a trace of blood and runs the risk of infection. This relationship is parasitism.

The same relationship exists between a lion and the antelope that serves as its food. We call this predation, with the lion being the predator and the antelope the prey. The difference between parasitism and predation is largely one of size. If the predator is smaller than the host, as with *Plasmodium*, *Taenia*, or *Clonorchis*, we speak of the relationship as parasitism. If the predator is nearly the same size or larger than the prey, we speak of predation.

The various species of antelope grazing in the same area are in competition to the extent to which they seek the same food plants.

Since all species are part of a complex web of life, it is usually impossible, except in carefully designed laboratory experiments, to find simple interactions involving only two species. Consider the following example, which is a simple interaction involving three species.

Bamboo—rats—people. In parts of India there are plagues of rats that seriously damage the crops after the bamboo blossoms (Marden, 1980). Individual plants of the bamboo, *Melocanna baccifera*, flower in synchrony after a vegetative period of about 30 years. Abundant fruit are produced and the plants die. In the one year when this happens there will be a sudden and large supply of food available for those species that find it acceptable. Rats are such a species. The rat population is generally kept within limits by many factors, the availability of food being the most important. During the year of the bamboo fruit, food ceases to be a limiting factor and the rat population rapidly increases in size. The food supply, though bountiful, lasts for a single season. The result is a large population of rats and the following year they are hungry and must go where the food is—to the farmer's crops.

Prior to the year the bamboo flowered, the rats competed with one another for food and their numbers were limited by predation, parasites, disease, a space to live, and so on. When the year of the bamboo fruit came, intraspecific competition for food became very much less. When this food supply was exhausted, intraspecific competition became more intense. Another type of competition also increased: the rat-human competition for the crops in the farmer's fields.

An important aspect of this complex interaction among bamboo, rat, and people is the short generation time of rats. During the period of abundant fruit the rats have time to raise several generations. Before adding this bit of information, ask your students if they would predict a population explosion of elephants when the bamboo blooms, assuming that the elephants would eat the fruit. Once again, try to keep the student's brains involved during the lecture period. They will not always come up with the answers but the effort itself is of the greatest importance.

Connell's barnacles. The zonal distribution of intertidal organisms has been mentioned before. Connell (1961*a*, 1961*b*) has some interesting observations and experiments that help to explain the zonal distributions of organisms and assess the role of competition.

On the southwest coast of Scotland there are two common species of barnacles that are restricted almost entirely to different microhabitats. *Balanus balanoides* is the more abundant of the two, forming an almost continuous mass on the rocks from the mean low water spring tide (the lowest of the low tides) up to somewhat above the mean high water neap tide (the lowest of the high tides). *Chthamalus* (pronounced "thamalus," mercifully) *stellatus* is restricted to the narrow zone between the mean high water neap and mean high water spring tides. Thus it is covered by the sea less of the time but it is kept moist by spray from the nearly constant wave action.

Adult barnacles are fixed in place, so it was possible for Connell to map the positions of individuals and to measure their growth and survival. It was possible also to

move rocks with barnacles to various sites to test the role of place, etc. Barnacles produce free swimming larvae, which eventually settle on rocks or other structures in the water. The larvae of the two species can be distinguished and so Connell was able to ascertain their attachment sites.

There are various hypotheses that can be suggested to explain the almost completely different zonal distribution of the two species.

1. *Chthamalus* might not be able to withstand long periods of immersion; hence, can survive only in the uppermost zone.

This hypothesis was tested by observation and experiment. There were a few sites where *Chthamalus* larvae had settled in a lower zone. Eight such sites were identified and divided into two areas. In both areas the precise distributions of the two species was mapped. One area was left alone but in the other area all the *Balanus* were removed, in order to have a test site with *Chthamalus* alone, not a site with interspecific competition. The general finding was that *Chthamalus* survived and grew well at the lower sites if *Balanus* was excluded. When both species were present, the *Chthamalus* were slowly overgrown or crushed by the *Balanus.*

2. *Chthamalus* might not be able to compete with *Balanus* in the intertidal zone.

This hypothesis was tested in part by the observations and experiments for the first hypothesis. Connell made additional observations. First he had to establish whether or not *Chthamalus* competed with itself. In areas from which *Balanus* had been removed he found that during an entire year only 6 deaths in 167 animals could be ascribed to intraspecific competition. When the two coexisted, however, *Balanus* grew faster than *Chthamalus* and either overgrew, uprooted, or crushed it. "Interspecific competition between *Balanus* and *Chthamalus* was . . . a most important cause of death of *Chthamalus.*"

3. A third hypothesis is that the larvae of *Balanus* and *Chthamalus* attach only where the adults are found.

Careful observations proved this not to be the case. The larvae of both species settled over much of the intertidal zone although *Chthamalus* did prefer somewhat higher places.

Connell made so many interesting observations that his paper provides much material for an inquiry approach. For example, you may wish to adopt a Socratic stance and ask your students to deal with this observation. One of these species has its center of distribution in the Mediterranean and is near its northern limit in Scotland. The other species ranges from the Arctic Ocean to northern Spain.

Can your students predict which species has which distribution? *Balanus* is the Arctic-Boreal species and *Chthamalus* is the Mediterranean species. Your students might have reasoned in this manner. Since *Balanus* may be assumed to be the more cold-adapted species and since *Chthamalus* is near its northern limit in Scotland, we might infer that *Balanus* is living in an environment more to its liking. It is able, therefore, to out-compete *Chthamalus* in the more desirable intertidal zone. *Chthamalus* would have only the less desirable sites and could even be superior there by being able to survive the hot, dry times in summer when the tide is out.

Starfish and their food. Another example of an interesting problem for students to consider emerges from some observations and experiments by Robert T. Paine (1966).

It has been emphasized several times in this essay that various factors tend to limit the populations of putative competitors to an extent that decreases or eliminates their competition for the same resource. This hypothesis can be tested in some carefully selected situations.

On the Pacific Coast of Washington there is one food web that consists of nine prey species and two predators. The prey consist of five species of mollusks, three acorn barnacles, and one goose-necked barnacle. Four of the prey species are eaten by the mollusk, *Thais.* The top carnivore is the starfish, *Pisaster ochraceus,* which eats all nine prey species plus the predator *Thais.*

The nine prey species occupy the same area, so to some extent their niches over-

lap. What would occur if *Pisaster* was not present? Would the other species remain the same or would competition for space and other resources become so intense that some species would be eliminated?

We can seek an answer by formulating this hypothesis: the coexistence of ten species that are prey for *Pisaster* is a consequence of their population sizes being controlled by the *Pisaster* and hence their is little interspecific competition.

An obvious deduction from the hypothesis is: if predation by *Pisaster* is the main factor controlling population sizes of the prey species, then removal of the predator should result in an increase in size of the prey populations and the occurrence of interspecific competition.

Paine selected an experimental site that extended along the shore for eight meters and had a vertical dimension of two meters. The adjacent, similar area was used as a control. Beginning in June he removed all of the starfish from the experimental site and continued to keep them out. By September from 60 to 80 percent of the experimental area was occupied by a single species—one of the acorn barnacles. By June of the following year the acorn barnacle had been replaced and the area was occupied almost entirely by one species of mussel and a few patches of goose-necked barnacles. In addition the algae were nearly gone and those species that could move, the chitons and limpets, had moved elsewhere—they had been crowded out.

The original hypothesis appears to be true. Competition for space, and possibly other resources, was largely prevented by *Pisaster* keeping the populations of the prey species below the level where competition would be severe.

Most surprisingly, it was observed that some other species, not part of the *Pisaster* dominated food web, also changed. In fact, half of these species disappeared following the removal of *Pisaster*.

Is there competition? The question whether or not animals of different species compete with one another has been vigorously debated in recent years. Some of the debate is based on differing definitions of "competition." Consider the situation on the plains of East Africa. All would agree that the various species of antelope would be in competition to the extent they sought the same food plants. But in what sense would the predator lion and the prey antelope be in competition? Some would say "Not at all" since the two species are not competing for the same resource. Others would say "Very much so" since both are competing for antelope—one for antelope as food and the other for an antelope body to be used to make additional antelope.

Such arguments tend to become polarized but it seems safe to say that some species compete with one another and others do not. In ecology we can expect to find the range of the possible if we look long and hard enough.

Laboratory experiments can be designed in such a way that two species are forced to compete under carefully controlled conditions in which food and space are the only limiting resources. Under these conditions competition may be intense. The outcome is nearly always the survival of a single species. This is very different from what transpires in nature, where there will be much less overlap of niches and, hence, a better chance of coexistence.

A nice perspective on the debate is provided by *Schoener (1982). See also Andrewartha and Birch (1954), Ayala (1972), Barbour, Burk, and Pitts (1980, ch. 5), Diamond (1978), J. B. C. Jackson (1981), R. S. Miller (1967), Milthorpe (1961), E. P. Odum (1971, pp. 211–228; 1975, pp. 128–140), T. Park (1962), Putnam and Wratten (1984), Ricklefs (1979, chs. 15–16), and Wiens (1977).

Weeds

A final topic that will test students' ability to suggest hypotheses is "weeds." That topic will also make a good transition to the major topic, human ecology.

One of the more interesting biological problems relating to weeds is as follows. Many European plants have become extraordinarily abundant in the United States. Some were introduced deliberately, others accidentally. They tend to replace the native species and, if they become a nuisance, we call them weeds. Why have

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FIG. 2. Weeds—colonizers of disturbed soils. The most conspicuous plants growing on this newly graded bank are the large, bushy Russian thistles (*Salsola kali*), a native of Eurasia. Other Eurasian species make up the bulk of the plants shown: mustard (*Brassica geniculata*), prickly lettuce (*Lactuca serriola*), wild oats (*Avena barbata*), ripgut grass (*Bromus rigidus*), lamb's-quarters (*Chenopodium album*), and knotweed (*Polygonum aviculare*). There are a few native species such as the flattened shrub at the right, dove weed (*Eremocarpus setigerus*) and the dark, spike-like telegraph weed (*Heterotheca grandiflora*). In less disturbed soils in this locality in southern California the Eurasian weedy species are infrequent or absent, except for *Brassica*.

very few American plants invaded Europe and replaced European plants?

What could be the biological basis of this Old World superiority? A field trip to a vacant lot, a recently abandoned farm field, or a newly made road cut will illustrate the phenomenon (Fig. 2). Alternatively, herbarium specimens can be studied in the laboratory. In either case the students should check in a local flora to determine the native home of the species collected and examined.

In an effort to formulate a hypothesis to explain the phenomenon, students might review what they already know about species and communities. One most important fact is that each species is adapted to a specific environment where it finds the resources required for life and has the ability to survive and reproduce. If it had not adapted, it would not be there. Little change in the status of the species within its natural community would be expected unless there was a significant change in the environment.

Then one should try to imagine how the weeds-to-be became established in the United States from the early 17th century onward. Some of them arrived with agricultural seeds brought by the early settlers, some arrived in the earth that served as ballast for the ships. Eastern America would not have resembled the plants' Old World home. Much was covered with an almost unbroken forest, not agricultural land. Some of the American Indians did farm but their numbers were small and their modification of the environment slight.

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During the following decades European settlers replaced American forests with European-style farms.

Over the centuries some of the European plants had evolved the ability to live in the disturbed farmland of Europe. This was a matter of appropriate genotypes having been selected for a new environment. These species, therefore, were preadapted for the newly disturbed farmlands in America whereas the native American plants were not.

Not all of the European plants are undesirable weeds. Most of our pasture grasses have been derived by further selection from those first perfected for Europe. Even the bluegrass of Kentucky, *Poa pratensis*, which should be as American as one can get, was introduced from Europe.

There is a similar story for the animal life of our cities. Your students might find it interesting to check on the original homes of the species that dominate the urban environment: rats, house mouse, house sparrow, pigeon, starling, house fly, and cockroach.

Weeds are fascinating biologically as you can see from E. Anderson (1954, ch. 2), W. P. Anderson (1983), *H. G. Baker (1974), H. G. Baker and G. L. Stebbins (1965, especially the article by Baker), Elton (1958), Georgia (1914), Harlan (1975, ch. 4), Harlan and de Wet (1965), *T. A. Hill (1977), Holzner and Numata (1982), Holm *et al.* (1977, 1979), Hooker (1853), L. J. King (1966), Mack (1984), E. J. Salisbury (1961), Silverman (1977), Zimdahl (1980), and van der Zweep (1982).

Fundamentals of ecology—a summing up

The more important concepts of general ecology that are critical for understanding human ecology have been covered in this first section. An attempt has been made to link each concept with its evidential basis. If this can be done successfully the concepts become much easier for the student to understand and remember.

The first main concept to be stressed is the absolute dependence of organisms on external sources for substance and energy. The substances consist of those elements that are common in the earth's crust: mainly C, O, H, N, S, and P but in addition many more collectively known as the micronutrients.

Second: these elements cycle between the living and non-living sectors of the ecosystem in complex interactions of plants, animals, and microorganisms. These interactions result in near constancy within the ecosystem.

Third: the major sources of the energy required for life is that of sunlight trapped in photosynthetic reactions. Only green plants and a few chemosynthetic organisms are able to use energy from non-biological sources. They are the autotrophs.

Fourth: the heterotrophs (animals, fungi, and many microorganisms) rely on the autotrophs for much of their energy and the substance that forms their bodies.

Fifth: the basic trophic level consists of green plants and chemosynthetic organisms. They are the producers. They serve as food for the primary consumers, mainly herbivores, of the next trophic level. The primary consumers are consumed by the secondary consumers, mainly carnivores.

Sixth: as the energy of food passes from one trophic level to another, most is lost as heat and only about 10 to 20 percent is available for the next consuming trophic level.

Seventh: in theory, all organisms have the ability to reproduce at rates yielding populations that would soon outstrip the resources required for life. In practice the many constraints in the environment—inadequate food, unacceptable climate, predation, disease, lack of a place to live, competition—tend to keep the population in check.

Eighth: mutation and natural selection have adapted each species for a highly specific way of life, the species's niche.

Ninth: the force of evolution diversifies the niches and a maximum portion of the environment becomes available for life.

Tenth: coexistence of two species is possible only if each has its specific niche with specific requirements for resources. Evolution tends to decrease the amount of overlap between niches and hence reduce the degree of competition.

Eleventh: the organisms of the ecosys-

tem are dependent on one another to varying degrees. None can live alone, so the health of the ecosystem becomes a general requirement for life.

And why not read G. E. Hutchinson's "Homage to Santa Rosalia" (1959)?

Special topics I

Ecology is so broad a field, so close to personal experience, so approachable, and so important for the future of civilization that its consideration in a first-year university course can only be introductory and, because of time constraints, is apt to be inadequate. As a partial remedy for this problem, and to provide students with experience in writing and speaking, you might consider having your students give 10 minute presentations during the laboratory periods on well defined topics in ecology. These would supplement the material presented in lecture and lab and, if two were planned for each lab session, about 60 could be scheduled during the academic year. If the presentations were at the middle of the lab sessions they might be a relaxing break.

Modern higher education is often far too passive an affair for students. We must find ways for students to become more actively involved. It could be of enormous benefit to students if they were required to organize topics, prepare a short essay, and then present the material to the class. This procedure would have the additional advantage of keeping ecological data and themes in mind throughout the academic year.

If the size of the laboratory sections was about 16–20, each student would have the opportunity of presenting about three topics during the academic year. The approachability of ecology and the deep interest it has for many could introduce the student to a study that could continue for a lifetime and would be related to the many issues discussed daily in the news media.

At the end of each of the three major sections of this essay there will be a list of appropriate topics and references. Lest the project become a chore rather than a useful adjunct to the course, it might be expected that a student could base the presentation on a single reference. The more interested students might wish to do more.

In addition to this list of Special Topics relating to Part I of this essay, others can be selected from the many subjects already discussed. In addition, suitable topics appear frequently in journals such as *Scientific American, Natural History, Audubon, American Scientist, Science, Science 84* (and other years), *Discover*, and *BioScience*.

Honey bee navigation. Apis mellifera uses a variety of cues to navigate between hive and sources of food. This is an interesting topic for those of your students with a fair background in physics. See F. C. Dyer and J. L. Gould (1983).

Mycorrhizae and pine trees. Some gymnosperms and angiosperms will grow only in their "native soil" because that soil contains the species of fungi that will form mycorrhizae on the roots of the plants. The mycorrhizae play a key role in the uptake of inorganic ions and water. E. Hacskaylo (1972) and J. A. Vozzo and E. Hacskaylo (1971) describe the attempts to introduce pine trees to Puerto Rico and the lack of success until the proper fungi were also introduced.

Adaptation to desert conditions—annuals. Deserts are highly stressful environments for plants because of the deficiencies of water in soil and air and, in most instances, the intense heat. Yet at times the desert floor may be carpeted with flowering plants. See T. W. Mulroy and P. W. Rundel (1977).

Lichens—living together on bare rocks. This combination of an alga and a fungus allows life under severe conditions. See M. E. Hale (1974) or V. Ahmadjian (1982).

Lichens—indicators of air pollution. A literature based report could be combined with local observations. See D. L. Hawksworth and F. Rose (1976).

Symbiosis of reef corals and algae. One of the most effective and visible associations in the living world. See D. L. Taylor (1983) and Muscatine and Porter (1977).

The panda and its food. The panda feeds almost exclusively on one plant—the bamboo. This plant has some sort of "internal clock" that triggers forests of bamboo to blossom and die after a growth period that may last for decades. When the bamboo

dies, so does the panda. See J. L. Fox (1984) and L. Marden (1980).

The koala and its food. Another mammal with a highly restricted diet, in this case the leaves of several species of eucalyptus trees. See Degabriele (1980).

Survival: competition or predation. The changes in the number of species occupying a small island off the west coast of Mexico has been analyzed in terms of either competition or of predation by the introduced domestic cat. See J. R. Jehl, Jr. (1984). For other aspects of the question of whether or not there is competition see J. A. Wiens (1983) and R. L. Tilson (1983).

Weeds, those un-American plants. Weeds are almost always introduced species of plants that replace the natives and become pests. This occurs almost always on disturbed soils and presents an interesting biological problem: how can it be that these introduced plants, which have evolved in different environments, seem better than our own species, which should have adapted themselves to the local conditions? See R. N. Mack (1984).

Parasitic birds. Cowbirds lay their eggs in the nests of other species of birds. The foster parents raise the young cowbirds, which are usually the only nestlings to survive. Is this nest parasitism by cowbirds a factor in the current decline of eastern songbirds? See M. C. Brittingham and S. A. Temple (1983).

Riparian forests as nutrient filters. Forest along streams can prevent nutrients from over-fertilized agricultural land from polluting the waterways. See R. Lowrance *et al.* (1984).

Fire as an ecological agent. Fire plays an important role in determining which species are present and in the cycling of nutrients. See R. E. J. Boerner (1982).

Botanical changes in the last 11,000 years. Pollen analysis allows the determination of which species are present at any one time and this information suggests what the climate must have been. See T. Webb (1981).

Why deserts (usually) do not bloom. Their low productivity is due to insufficient water and nitrogen. See N. F. Hadley and S. R. Szarek (1981).

Where did I put that nut? Most animals rely on the food that can be obtained at the moment. Some can store any excess for future needs. See S. J. Shettleworth (1983).

How to avoid being eaten. Mollusks and echinoderms, not noted for speed, have behavioral mechanisms for avoiding predation. See H. F. Feder (1972).

How to get home, pigeon. The ability of homing pigeons to find their way home when released many kilometers away, in strange territory, has excited the interest of biologists for years. For some of the answers see W. T. Keeton (1974*a*, 1974*b*).

El Niño. Recent changes in the ocean currents of the Eastern Pacific have had profound effects on the climate and many marine and terrestrial organisms that depend on the sea. A change of a few degrees in the temperature of the ocean water shows how seemingly small differences in the environment have large consequences. See E. Edelson (1984) or T. Levenson (1983).

How trees defend themselves. They engage in chemical and biological warfare. See S. Brownlee (1983).

The destructive tent caterpillars. They are a serious problem for trees. See T. D. Fitzgerald (1983).

Interactions of microorganisms and human beings. For better and for worse. See P. M. Mackowiak (1983).

The Atlantic salmon. Its biology is changing probably as a consequence of overexploitation by human beings. See W. L. Montgomery (1983).

Internal clocks of human beings. They were set for a different time in human history. See M. C. Moore-Ede (1982*a*, 1982*b*).

Blanket bogs. These mats of peat reveal their history. See P. D. Moore (1982).

Dall's sheep. How they live in the harsh and difficult environment of Alaska. See G. Wuerthner (1982).

The medfly. A serious pest of citrus. See W. H. Jordan (1982).

Fallow fields and their birds. When farms are abandoned there is a succession of different plant communities as the land returns to a near-natural condition. Each community is home for a unique set of bird species. See W. E. Lanyon (1982).

Predators and their varying prey. What they

eat depends on what there is to eat. See A. T. Bergerud (1983).

Dutch elm disease. The attempts to control this pest, which changed the ambience of New England towns and villages. See G. A. Strobel and G. N. Lanier (1981).

II. THE TIME OF MAN

Among the fundamental facts of life for all species are two processes that determine the size of their populations.

1. Reproduction: Every species has a potential rate of reproduction that, in the absence of restraints, would tend to increase the population size to infinity.

2. Attrition: This potential increase is held in check by two main forces: destruction by other organisms (predation, disease organisms) or the lack of essential living conditions and resources (food, suitable climate, a place to live).

All species reflect the interactions of these two major processes, one tending to increase population size, the other to decrease it. The first process never dominates except for very brief periods of time. The second process leads to a common scenario. As a consequence, far more species have evolved and become extinct than now exist. Many of these cases are taxonomic extinctions, that is, one species evolved into another. Apart from these instances, however, there are many lineages that have simply passed from the face of the earth.

Evolution rewards success and the most precise indicator of biological success is the size of a species' population. The pressures on all animal species therefore will foster ways to avoid predation, survive disease, and secure the conditions and resources necessary for life. In doing so, the species become more abundant. But lasting success can never be achieved. The rewards of avoiding predation, surviving disease and obtaining more resources would be a population always increasing in size and always on the verge of insufficient resources.

Every organism responds to the environmental challenges of the moment with what it is and what it can do. It has been programmed during its evolutionary lineage by the genetic responses made by its ancestors to the environmental challenges of their times. New genotypes formulated in the gonads might be the wave of the future but that helps a living individual not a whit. When the lake dries up the fishes do not walk away as tetrapods. The dinosaur's lament "What has future evolution ever done for me?" applies to all organisms.

The flow of human history has been modulated by human ecology—our relation to the environment. Kings and conquerers come and go, making only a blip in human affairs, but our interaction with the environment exerts the most profound controls over the life of nations and their inhabitants. The understanding of the present must be based on knowledge of the past.

What it takes to be a man

For most of human life, species of the genus *Homo* were undistinguished primates. They were no match for the great predators nor could they avoid them by fleetness of foot. They must have been furtive, apprehensive creatures. Nevertheless they possessed the biological basis for eventually achieving a civilized state. This was not true of all primate species, let alone all mammals. Almost none of the mammals living today possess the biological prerequisites to develop a civilization and none could do it short of millennia of additional evolutionary change.

So what were the characteristics of the first species of our genus that provided the basis for our extraordinary cultural evolution? Or possibly we should turn the question around and ask what it is that makes the human species so exceptional and then ask what are the biological prerequisites?

Better yet, have the students consider this question: What do *they* believe are the criteria of being human? Once such a list has been established, what do they suggest are the morphological and physiological features that the very early species of *Homo* must have possessed that would permit us to achieve our present state?

Students will be able to suggest the more obvious biological features of civilized human beings: intellectual ability; use of

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complex language and writing to transmit information among individuals and between generations; skill in the manufacture and use of tools; great ability to obtain food and other resources; ability to avoid becoming prey of carnivores; considerable ability to cope with disease-causing organisms; complex social structure; dependence of the young on parents for an extended learning period; great ability to control the environment or to adjust to it.

But are some features more basic than the others? Would your students accept the following statement? *The two most essential characteristics of the human species that have made civilization possible have been the ability to domesticate plants and animals in order to insure a more reliable supply of food and the ability to use sources of energy other than food to perform work.* Prior to developing these abilities, human beings were only slightly better than other animals in that they could use crude tools for protection and obtaining food. Raising more food and being able to use another source of energy made possible a great increase in population size, the formation of cities, divisions of labor and specialized work, communication, and all the features of early civilization. The prime non-food source of energy was fire, which to this day remains the most basic source of energy used by the human population.

What is being said is that human beings are more able than other animals, by several orders of magnitude, to secure the resources for life and to protect themselves from the attacks of other organisms.

Your students may see some of the limitations of my attempt to reduce all human superiority to two basic abilities. They may suggest other ways of looking at the uniqueness of the relations between human beings and the environment. All points of view should be accepted and regarded as hypotheses for interpreting the data to come. Nevertheless, we can organize our inquiry around my statement.

It will be interesting for your students to speculate on what must have been the anatomical and physiological characteristics of the most advanced pre-*Homo* primates that enabled them to cross the threshold into humanity. Different scholars place that threshold at different times in our history. It is now known that the use of tools began with the Australopithecines, the group that was to evolve into *Homo.*

Tools

What sort of an anatomy do we need to make and use tools? The answer may be developed by asking questions about other sorts of animals. Can horses, cows, fish, birds, dogs, and monkeys use tools? Part of the answer, "hands," should be obvious; not any sort of forelimb but one with movable fingers and an opposable thumb. The role of that thumb is often unappreciated by students. Suggest that they tape their thumb to the first finger and try a variety of manipulations: using a hammer, knife, fork, screw driver, saw, or long bow with the thumb immobilized.

Bipedal gait, which allows the free use of hands, is a closely associated characteristic. It may not be as obvious to students that eyes in the front of the head, which provide stereoscopic vision, are a requisite for doing delicate work with tools and hands. A well-developed brain is absolutely necessary if tools are to be systematically invented, made, and used.

A few other animals do use tools (Hall, 1963; Lawick-Goodall, 1970; Alcock, 1972). Some wasps use a pebble to pack soil (Peckham and Peckham, 1898); the Galapagos woodpecker finch uses sticks to extract insects from holes (Lack, 1947, 1953); an orangutan showered Schaller (1961) with sticks and branches; sea otters use rocks to free abalones and to break open clams (Fisher, 1939); chimpanzees, especially when tamed, can become quite skillful in using a variety of tools (review in E. O. Wilson, 1975, pp. 172–175); and there is some evidence that polar bears pick up chunks of ice to bash in the heads of sleeping walruses (Harington, 1962).

In these examples the tool is a natural object already at hand. The stick or stone is an extension of the animal's appendages to secure food, repell Schaller, or pack down the soil. Tools allow the animal to accomplish tasks more effectively than with the appendages alone.

The earliest tools used by our ancestors

must have been naturally occurring sticks, stones, and shells. Experience would have shown that some sticks or some stones were better for a given task than others. A heavy stone could be hurled at nearby prey species or used to crack a nut with a thick shell. A smaller stone would have to be used for more distant targets. A rigid, pointed stick would be more useful than a flexible, blunt one for digging roots. One might have to look around to find the proper naturally occurring tool for the job.

One of the most momentous events in human history occurred when some Australopithecine genius realized that, if a pointed stick was not readily available, *it could be made.* This event probably occurred at least two million years ago. Similarly if one could not find a stone with a sharp edge to cut through the hide of even a moderately sized mammal, maybe one could break a stone in such a way as to give a sharp edge.

Tools allow the user to perform tasks that would be difficult or impossible to accomplish without them. An arm might not be able to reach a distant animal that could serve as food, nor could the legs permit one to run rapidly enough to overtake the prey but a thrown rock, boomerang, spear, or arrow could. Teeth and hands might not be able to crush a skull or the thick shell of a nut, but a rock or hand-ax could.

The earliest tools were thus extensions of functions performed by arms, legs, and teeth. In the distant future tools (broadly defined) of other sorts were to expand the effectiveness of other parts of the body: telescopes, microscopes, TV, radar, and spectacles extend the usefulness of eyes; telephones and radios extend the effectiveness of ears; power tools and weapons of arms; bicycles, ships, automobiles of the legs; and computers extend the effectiveness of the mind.

There must have been a gradual technological evolution from natural stone to the first crudely shaped tool. The change was so gradual, in fact, that archaeologists may argue whether or not a given object is natural or man-made. How can one decide?

The earliest objects that are generally accepted as tools made by human beings are the pebble tools first studied by the Leakeys at the Olduvai site in Tanzania (M. Leakey, 1966, 1970). Subsequently similar simple tools have been found in Europe and Asia. These tools consist of a small rock from which flakes have been struck. Flaking provides a rough cutting edge. This beginning of technology can be placed roughly at 2–2.5 million years ago in what is known as the Paleolithic Period or Old Stone Age.

Stone tools provide the best evidence we have for how human beings lived in the Paleolithic because they have survived whereas any objects made from wood, bone, reeds, or skin have perished.

This beginning of technology was not followed by a rampant rise to civilization. For about a million and a half years there was little change in the quality or variety of these crudely fabricated tools of the Old Stone Age. Then about half a million years ago there appeared the hand-ax, a generalized tool that was used over a wide area that includes parts of Africa, Europe, and Asia. The hand-ax was formed by chipping flakes from a core of stone, such as flint, until an oval or triangular tool with an edge all around was formed. Despite the name, the continuous edge makes it unlikely that this tool was held in the hand and used as an ax. More likely it was a cutting tool. Hafting came later.

Stone tools and those made of wood and bone continued to be widely used, improved, and perfected for new purposes down to recent times. Until European cultures reached them, much of Africa, some remote parts of Asia, and all of Australia and the Americas were in the Stone Age. The tools of the Australian Aboriginals were much like those of the early Paleolithic. Some Stone Age people were able to achieve high civilizations without the extensive use of metals for tools: the Incas of Peru, the Aztecs of Mexico, and the Mayas of Central America. The Aztec priests used exquisitely made stone knives to cut out the hearts of their living human sacrificial victims. Civilization need not depend on the extensive use of metal. Long

after copper, bronze, and even iron became available, stone tools continued to be used. After all mill-stones are made of stone.

The ecological importance of tools. Tools greatly increased the chances of survival for early human beings. Alone, but especially in small groups, hunters were able to defend kith and kin from the large predators and to kill even the largest mammals, the elephants, for food. They could obtain edible roots with primitive picks and hoes. Small branches could be cut more readily and fashioned into shelters. Had an elephant, or even a deer, died of a heart attack in front of a person in the days before cutting tools were available, the carcass could not have provided food. With teeth and hands alone, the thick skin could not have been broken. A well-known anthropologist once tried to tear the skin of a cat with his teeth and hands alone; he couldn't. Cutting tools, even the simple pebble tools, would have aided greatly in cutting the skin. In time it became common to remove the skins of mammals carefully and use them for a great variety of purposes: clothing, shelters, pouches, shoes, shields, rope, ornaments, and containers.

Thus tools helped to avoid two of the important environmental hazards tending to make life short and unpleasant: being eaten by something else, or starvation. With those dangers lessened, population size tended to increase.

Statements about the size of the human population in the Paleolithic are merely poorly educated guesses. One can do no more than combine guesses about "what must have happened" with information about the geographic distribution and abundance of artifacts. J. Z. Young (1971, ch. 25) estimated that the human population numbered 100,000 at the beginning of the Paleolithic and that it had grown to between 5 and 10 million by the end. G. Clark (1967) estimated that there were 1 million human beings in the Middle Paleolithic. The start of the Paleolithic can be set at about 2 million years ago (new evidence is suggesting ever earlier dates) and the end at about 12,000 years before the present. Thus if we began with a population size of 100,000 and increased it by only 2.5 to 5 individuals per year, we would obtain the estimated size at the end of the Paleolithic. The increase would not be constant, of course, but would depend on the size of the population at any one time. The estimated increase during the Paleolithic would be accounted for by a rate of increase of about 2.4 individuals per year for each million persons! Dummond (1975) estimated that the human population at the end of the Paleolithic was about 3 to 5 million and that the rate of increase was between 7 and 15 individuals per year per million human beings. Our ancestors were hardly having a population explosion but at least they kept the lineage going.

Fire

The next tremendous discovery of our Paleolithic ancestors was how to use fire (Oakley, 1955). Fire was the alternative source of energy, apart from food and sunlight, that was to carry us to a position of immense control over some aspects of nature. It can be maintained that the *use* of fire is the first unique human discovery. The use of tools has its antecedents in other animals. To be sure, other animals almost never manufacture tools, yet one can stretch the point and say that the orangutan that broke off a stick to throw at Schaller was "making" a tool.

There is no doubt that the use of fire is uniquely human. No sea otter or polar bear ever made a fire to cook abalone or walrus.

Fire is so difficult to start that it seems almost certain that human beings first obtained it from naturally occurring fires: those started by lightning, the hot lava of volcanoes, or by friction of tree limbs rubbing together. Until fairly recently, once a fire was started the tendency was to keep it burning if at all convenient. Thus, one of the essential characteristics of a good wife was that she saw to it that "Her lamp does not go out at night" (Proverbs 31: 18—the King James Version reads "her candle goeth not out by night" but that is an error of translation; the ancient Israelites did not have candles).

All of the fires of the Paleolithic have been extinguished so we must rely on indirect evidence for their use. Students should

be able to suggest some types of evidence. Even if they cannot, the effort of thinking about the problem is worthwhile. Some majors in Art History may know of the cave paintings at Lascaux. These Cro-Magnon murals (Bataille, 1955) are deep underground and could not have been painted without artificial light. Hence, fire must have been used. The oldest lamps so far discovered are from the caves at Lascaux, where they are abundant.

Other evidence, such as hearth sites in caves and other shelters, suggest that the fire was used for warmth, cooking, light, and probably protection. The fact that American Indians and other native peoples used fire to flush game or enemies permits us to reason, by analogy, that this was done in the Paleolithic as well. Fire can be used also to harden the pointed ends of wooden spears and to fracture stones to obtain sizes and shapes suitable for tools.

One cannot overemphasize the importance of fire in increasing the resources available for human beings. It is the source of power that made civilization possible. Once again we find that certain biological conditions must be met before a species can use fire. Ask you students to suggest what makes it possible for them to use fire. The morphological features that made it possible for our ancestors to invent, manufacture, and use tools (dextrous hands, well developed brain, eyes placed in front of the head allowing binocular vision) were necessary to permit the use of fire. There is an additional special feature, however. Fire can be used only by animals of at least moderate size. Think of some of the problems that a mouse, or even a cat, would have in trying to make and maintain a fire—and not get singed.

The oldest known use of fire yet discovered comes from the Chesowanja site in Kenya (Gowlett, 1984*a*, p. 46). The date is about 1.5 million years ago. Here and elsewhere the evidence for the deliberate use of fire consists of hearth sites with the remains of ashes or charcoal, and burnt bones.

This matter of "the oldest known . . ." is important for students to understand. If, for example, the beginning of the Paleolithic is defined as the time when tools were first manufactured, the date will always depend on what the archeologists have found. Before the Leakeys began their discoveries in East Africa, the Paleolithic was assumed to have begun about 1 million years ago. Now the date is generally accepted as 2 million years and the evidence is beginning to accumulate that 2.5 million years might be a better estimate for the onset. There is no way to give a precise answer to the question, "When did the manufacture and use of tools begin?" The best that we can say is that the "oldest known date is . . . ."

Cooking. From the earliest times one of the most important uses to which fire was put was cooking. The importance was not only that meals became more tasty but that cooking could make some otherwise inedible foods edible, kill any parasites in the food, and retard decay.

Many plants have evolved devices that serve to repel consumers. Spines, thick bark, irritating sap, and innumerable toxins make some plants difficult or unpleasant to eat. Many of our crops belong to genera and families of plants in which some of the wild species are poisonous. It seems probable that the crop species have been selected to eliminate the toxicity. Some are still highly toxic—the story of manioc will come later.

The toxins of many wild plants (those were the only ones available in the Paleolithic) are destroyed by heat. Toxic proteins are denatured; other toxins are destroyed by oxidation or other reactions; if food is boiled in water, the toxins may become concentrated in the water, which can be decanted (Leopold and Ardrey, 1972; Ames, 1983).

Cooking does many other things to food, some beneficial, some not. It is an efficient short-time preserver of food and, in some instances, can preserve food for long periods. Some plant and animal material can be dried over fire and, with the moisture removed, can be immune to decay for long periods of time. Cooking destroys those enzymes in animal and plant tissues that result in autolysis. Microorganisms of decay are likewise destroyed.

The seeds of wild grains, which were to become the cereals that are still our basic foods, provide very little nutrition unless cooked. When starchy foods are boiled the starch granules are ruptured and digestion is greatly facilitated.

The use of fire, then, began to increase the food resources available to human beings in the Paleolithic. Little is known about what was cooked and what was eaten raw. Meat could have been placed on a stick that was held close to the fire. The seeds of cereals could have been roasted by placing them on stones close to a fire. Eventually, boiling food was to become important. For that, however, some type of receptacle was required. Tightly woven baskets, especially if lined with baked clay, could have been used for boiling food. In this case the container was not placed on the fire but the water was heated by placing hot stones in it.

Heavy stone and clay vessels are not practical for wandering hunter-gatherers. Bowls made of stone seem to have been used until about 9,000 B.P. when pottery made from clay started to become common. These utensils belong to the Neolithic, when human beings began a more settled life.

In recent years a surprising new technique has begun to tell us a great deal about the food of hunter-gatherers. This is the study of coprolites (fossil fecal material) where one can find evidence not only of the food eaten but of parasitic organisms as well. See Wilke and Hall (1975), Heizer and Napton (1969), and Fry (1980).

Paleolithic culture

The transition from *Homo erectus* to *Homo sapiens* occurred about 400,000 to 300,000 years ago. Evolution continued slowly and by the latter part of the Paleolithic the human populations reached the biological stage of modern human beings in structure, brain size, and appearance. Biological evolution was to continue but the dominant force was to become cultural evolution.

The Paleolithic of the anthropologist is roughly equivalent to the Pleistocene of the geologists. This was the period of repeated advances and retreats of ice sheets across the continents of the Northern Hemisphere. There is evidence of human remains from sites not far distant from the edge of the ice. This was a tremendously different environment from the tropics that had been the home of human beings for so long. It could mean that the pressures of an increasing population were forcing human beings to seek new resources and places to live.

This was still the Stone Age but the variety and excellence of tools had reached a high level of technology. Flint had become the favorite stone. From it were manufactured scrapers for preparing skins; many sorts of tools with cutting edges such as axes, knives, spears, arrow heads; and burins for working bone. Burins were used to shape bone into needles (with eyes!), awls, projectile points, harpoons, and ornaments. Artificial dwellings, including tents, were used.

For the first time we have evidence of concerns beyond food and protection. It should be interesting for your students to speculate on the meaning of these new aspects of human life: the ceremonial treatment of death and the expression of emotion in the arts. Thus, there are examples of deliberate burials going back for about 100,000 years. In the oldest so far found the bodies are carefully oriented in an east-west direction. It became usual for ornaments and other objects to be interred with the dead. There are remains from these millennia of musical instruments, carved images such as the Venus figurines, and cave paintings (Breuil, 1952; Bataille, 1955; Graziosi, 1960; Bandi *et al.*, 1961; Leroi-Gourhan, 1967; Ucko and Rosenfeld, 1967).

What can one say about the thought patterns of individuals doing these things? What could have been going through their minds when they took the trouble to bury a family or band member and to place valuable tools and ornaments in the grave? Gowlett (1984*b*) suggests some of the answers.

Social organization

If we use the evidence of recent cultures in an equivalent stage of development, it seems probable that people of the late Paleolithic moved in bands that could have numbered 200–500 individuals. Although any single human being would have been hard pressed in an encounter with the great carnivores or the elephants, mammoths, and other large mammals, a band of human hunters could prevail. In a similar way a group of hunters would have a greater chance of success than would a lone individual. In groups of this sort, it is a reasonable guess that there would have been at least some division of labor. The care of children probably fell largely to the women who profited by the assistance of others in the group who were freer to obtain food by hunting and gathering. Some members of the group might be better than others in making tools, others in using them.

In the period we are discussing, humans were still in a pre-agricultural period when food was obtained by hunting and gathering. Many species of wild animals and wild plants would have been sought. This type of economy requires a very large area. H. Brown (1954) estimates that "about two square miles [5 square kilometers] of fertile land in a natural state are required to support a single individual." Schwanitz (1966) puts the figure at roughly 20 square kilometers.

Social groups are most effective when there is some degree of leadership, so we might guess that the antecedents of generals, kings, and priests are to be found among Paleolithic people.

Social cooperation combined with a much improved tool technology were aspects of cultural evolution that increased the possibility of obtaining resources from the environment and protection of the members of the social group. In fact, the success of late Paleolithic people in obtaining resources may have led to such an increase in their numbers that the environment could not support them. There is some evidence that this may have been so because about 40,000 years ago not only were the Old World tropics and much of Europe and Asia south of the Pleistocene ice sheet inhabited, but there were mass movements into Australia and the New World. The world was filling up.

References to the Paleolithic Period

The literature pertaining to the Old Stone Age is tremendous. This is not surprising, since this was the time when our lineage passed to the stage of modern human beings. The following is a sample. *Bailey (1983), Bartholomew and Birdsell (1953), Bender (1975), Bicchieri (1972), Bigelow (1969), Bishop and Clark (1967), Bordaz (1970), Bordes (1968), Brace, Nelson, and Korn (1971), Braidwood (1967), British Museum (1975), Browman (1980), H. Brown (1954), R. W. Brown (1981), Butzer (1971), Childe (1942), Chinese Academy of Sciences (1980), G. Clark (1967, *1969, 1970), G. Clark and Piggott (1970), le Gros Clark (1967, 1971), Clutton-Brock and Grigson (1983), Coon (1971), Daniel (1955), *C. D. Darlington (1969), Dennell (1983), Densmore (1928), Dimbleby (1977), Dixon *et al.* (1968), Dornstreich (1973), Fairservis (1975*a*), Foley (1984), Forde (1963), *Gowlett (1984*a*), *Hawkes (1963*a*), Higgs (1972, 1975), Hodges (1971), Howells (1973), Hvarfner (1965), Isaac (1981), Isaac and Leakey (1979), Isaac and McCown (1976), Jolly (1972), P. R. Jones (1981), Lancaster (1968), M. D. Leakey (1966, 1970, 1979), *R. E. Leakey (1981), R. E. Leakey and Lewin (1977, 1979), R. B. Lee and de Vore (1968, 1976), McEvedy (1967), Marshack (1972), Milisauskas (1978), Mulvaney (1975), Murdock (1967), Oakley, (1969, 1981), Pfeiffer (1972, 1977), Pilbeam (1972), Ronen (1982), Rukang and Shenglong (1983), Sahlins (1960), C. Singer, Holmyard, and Hall (1954), Stigler *et al.* (1974), Trinkaus and Howells (1979), Walker (1981), Washburn (1960, 1978), Wendorf and Marks (1975), R. V. S. Wright (1977), *J. Z. Young (1971, chs. 32–37), and J. Z. Young, Jope, and Oakley (1981).

Two interesting fictional accounts of what life in the Paleolithic must have been like are given by Auel (1980, 1982).

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General references to archaeology

Many of the topics in Part II will not only be human ecology but anthropology as well. Some general references to this field are: Baillie (1982), J. Baker and Brothwell (1980), Brothwell and Higgs (1970), Butzer (1971), Ceram (1967), Daniel (1964), *Fagan (1981), Fitting (1973), Hole and Heizer (1973), Ingersoll *et al.* (1977), Janssens (1970), Joukowsky (1980), Leone (1972), Neill (1978), Olin and Franklin (1982), C. Renfrew (1979), and Shackley (1981).

The agricultural evolution—the early Neolithic

The domestication of plants and animals eventually insured a more abundant and reliable food supply for a population slowly increasing in size. As Sir Leonard Woolley (1963, p. 363) put it, "instead of having to live where food abounded [man] made it abound where he lived." Agriculture represents the third and last of the great achievements of prehistoric human beings that enhanced survival of the human population. The first two were the manufacture and use of tools and the ability to use non-food sources of energy to produce heat and to do work.

Before the topic of plant and animal domestication is considered, it would be profitable for your students to discuss the limitations on everyday life in late Paleolithic times when the economy was based on hunting and gathering. Think of the amount of space required by a single individual. It would have to be sufficient to support populations of wild animals and plants that could be harvested for human food and yet not be overexploited to the point of extinction.

Zeuner (1963) reminds us "that the pygmies of the Congo forest have to change their abodes once every few months because they have exhausted their food supply completely by hunting and food-collecting, in spite of the fact that their communities consist of no more than family groups."

For people living in arid regions, the distribution of water holes could be limiting. Where water is scarce hunters and gatherers would be restricted to areas where water can always be reached at least once a day. What, for example, would be the area that a hunter or gatherer could reach in a walk of about three hours? Under such conditions would a sedentary life have been possible? Could there have been villages and cities? The answer to both of those questions at the end of the Paleolithic, about 10,000 years ago, was "no." But momentous events, both geological and human, were underway and the answer was beginning to be "yes."

About 15,000 years ago the great ice sheets still covering the northern parts of Eurasia and North America began to melt. During the next 5,000 years the ice sheets shrank to an area nearly the same as they cover today. So much of the earth's water was contained in the ice sheet that, when at its maximum, sea level was about 130 meters (about 425 feet) lower than today. The Atlantic coast of the United States was much farther to the east. England was part of the European continent but it gradually became an island as the ice melted. Even today there is still enough water in the Arctic sea ice, in glaciers, and especially in the Antarctica ice cap that, should all melt, many of the world's major cities, which are often in coastal plain zones, would be drowned.

As the Pleistocene (and Paleolithic) slowly came to an end, vast areas, previously scoured of all life by the grinding of the ice sheets, were uncovered and began to be repopulated by plants and animals, including human beings. This was a slow process. The pioneer plants would have to begin the process of forming soil. It required centuries to bring the land to the condition we see today.

Cultural evolution had been occurring at an ever-faster rate during the last millennia of the Paleolithic. The Paleolithic cultural period and the geological Pleistocene period closed at about the same time—10,000 years ago when the ice had retreated to its present position and human beings were to begin the so called "Neolithic Revolution" that carried our nomadic Stone Age hunter-gatherer ancestors to the

earliest stages of civilization. And, once again, this involved a variety of new discoveries that provided more food and protection. This led, inevitably, to a larger population size and to greater pressures on the environment for the necessities of life. Human ecology was becoming more complex.

The domestication of animals and plants

The first major accomplishment was the domestication of those species of plants and animals that, to this day, remain the major sources of our food. The direct ecological importance of this event was that, in time, it provided a more reliable and more abundant supply of food. An indirect ecological consequence was that it allowed increasingly large numbers of individials to stay in one place. This, in turn, allowed a more stable society; increased interactions among human beings; better protection from wild animals and enemies; a division of labor that permitted the development of specialized crafts, industry, and occupations; increased leisure that could be devoted to recreation. thinking, and the arts and sciences; and the development of a hierarchical society. Quite simply, civilization was made possible by the domestication of plants and animals.

The species that were domesticated, not surprisingly, were the wild species that had served as food for the hunter-gatherers. In view of the very slow cultural evolution from the earliest tool makers to the end of the Paleolithic (about 2 million years), the domestication of the major crop species was accomplished in a very short time. In the Old World it took place between roughly 10,000 and 7,000 years ago.

The study of coprolites is continuing to provide considerable information about the food eaten by prehistoric human beings (Wilke and Hall, 1975; Heizer and Napton, 1969). Evidence is replacing conjecture.

The Near East: cereals and pulses. The Near East—near to Europe, that is—is bounded on the west by the Mediterranean and on the east by the high plateau of Iran. It is a region of great importance in human history. Much of it is semiarid or desert. The early stages in the domestication of plants are thought to have occurred in a broad band of better watered land, called the Fertile Crescent. This stretches along the foothills from southern Jordan and Israel, north to southeast Turkey, and then southeast along the border region between Iran and Iraq. The average rainfall is 30 cm (12 inches) or better. This is open country with few trees.

In recent years archaeologists have worked intensively in this area, hoping to learn what they could about the origin of agriculture. The region was not chosen at random. Long before there were any useful archaeological data, de Candolle, the first important student of plant origins, thought that some part of the Fertile Crescent might have been the site(s) of the first domestications of wheat and other food plants.

His reasoning is a fascinating example of how one can proceed with a scientific analysis when a field is new and the data meager. According to de Candolle (1886, pp. 354–359) "We have two methods of discovering the home of the species previous to cultivation . . . first, the opinion of ancient authors; second, the existence, more or less proved, of wheat in a wild state in a given country."

His hypothesis was that a plant, wheat in this case, would have been first domesticated where wild wheats served as food. In de Candolle's time wheat was grown throughout the temperate regions of the world. If wild wheat had a similar distribution, it would be impossible to determine the place(s) of early domestications. On the other hand, if wild wheats were found in only one area, it would be reasonable to assume that area was the site of its first domestication.

A survey of ancient authors gave a few clues. Berosus (available to us only as fragments in Herodotus) gave the earliest known historical account saying that wild wheat grew in Mesopotamia (Iraq). There were other ancient reports but de Candolle concludes, "Among all this evidence, that of Berosus and that of Strabo for Mesopotamia and Western India alone appear to me of any value."

De Candolle's second method was to

ascertain the present distribution of wild species. Only a meager amount of botanical work had been done in the Near East by the year de Candolle wrote. The only reliable report known to him for wild wheat was written by Olivier, about 1820, for Mesopotamia. De Candolle concludes, "It is remarkable that wheat has been twice asserted to be indigenous in Mesopotamia, at an interval of twenty-three centuries, once by Berosus, and once by Olivier in our own day . . . . It is infinitely probable that it was the principal habitation of the species in very early prehistoric times."

De Candolle used still another method to show that wheat must have been first cultivated at a very early date. He examined all the ancient languages then known and found that all had words, but *different* words, for wheat. "The manifold names of ancient languages must, therefore, be attributed to the extreme antiquity of its culture in the temperate parts of Europe, Asia, and Africa—an antiquity greater than that of the most ancient languages."

What tentative conclusions would have been reached had all the ancient languages had the same, or similar, names for wheat? Try that one on your students. A discussion will probably result in their having serious reservations about de Candolle's use of language as indicating the age of domestication of wheat.

Recent observations support de Candolle's hypothesis. Wild wheats have been discovered to grow abundantly in the uncultivated hilly regions of the Fertile Crescent (a fine map is in Braidwood, 1960). They belong to two species: wild einkorn (*Triticum boeoticum*) with a monoploid number of 7 chromosomes and wild emmer (*Triticum dicoccoides*) where N = 14. It is believed that wild emmer arose by hybridization of wild einkorn with the goat grass (*Aegilops speltoides*, N = 7), followed by a doubling of the chromosomes to form an allotetraploid.

Harlan (1967) made some fascinating observations at a site in southeast Turkey where wild einkorn grows in abundance. He looked across the fields of this food of Paleolithic human beings and asked several questions. "How attractive would a natural stand of wild einkorn be to a hungry food-gatherer? How much food could he expect to harvest in a day or season? What tools would he need? Could he harvest the wild cereals with flint sickle blades?"

First Harlan tried harvesting with his bare hands. He pulled off the heads and found that he could harvest one kilogram of grain per hour. Next he placed a genuine Neolothic flint sickle blade in a modern handle and found that it was as efficient as a modern steel sickle. This was Harlan's important conclusion:

> A family group, beginning harvesting near the base of [the mountain] and working slowly upslope as the season progressed, could easily harvest wild cereals over a three-week span or more and, without even working very hard, could gather more grain than the family could possibly consume in a year.

Harlan had harvested a splendid food as far as nutritional qualities are concerned. When compared with modern high quality red winter wheat, it proved to have less water and carbohydrate and more ash and protein. It was difficult to prepare however. Both einkorn and emmer have glumes that must be threshed out. This could be done with a large wooden or stone mortar and pestle or by roasting. The final product could be eaten after roasting, made into a porridge or, with a few pieces of meat, into soup. Harlan tried the last. It was delicious.

Genetic changes accompanying domestication. Natural and artificial selection have very different outcomes. This is not surprising since one is directed toward the survival of the species in nature and the other for the convenience or survival of human beings. Natural selection tends to make a wild species better adapted to the local conditions. The goal of artificial selection is to produce better crops, stronger beasts of burden, or more beautiful roses. The cereal grains can serve as an example of these two sorts of evolutionary change.

In wild populations considerable genetic variability is an advantage. In those years when the climate is atypical, many individuals would probably perish but a few with

somewhat different genotypes might survive. Variability allows different individuals of a plant species to grow over a broader range of soil that varies in moisture content, chemical composition, exposure, and other microenvironmental conditions. For cultivated plants, the farmer seeks to maintain more constant conditions: soil tilled, weeds controlled, fertilizers added. The farmer seeks uniformity and the crop plants become adapted to the conditions maintained by the farmer.

In wild plants it is often advantageous for the seeds of a single plant to mature at different times. This increases the chances that at least some of the seeds will survive. With cultivated plants on the other hand, harvesting is more economical if all the seeds mature at the same time.

In the wild cereals, the seed heads tend to shatter, which means a considerable loss to the gatherer, and they also mature at different times. In the cultivated cereals, the seeds are held until they are harvested. In wild populations the seeds are covered by a tough, protective coat or hard glume. These are greatly reduced in the cultivated varieties, thereby making the preparation of the grain for food much easier. The genetic differences between shattering and non-shattering involve two loci; between hard and soft glumes a single locus.

Some of the selection that converted the wild populations to the cultivated condition may have been incidental to the process and not the results of deliberate decisions of the first farmers. The seeds that were plucked from the plants would, obviously, not be those that had been shed. Thus the unconscious selection would be for those genetic types that held the seeds. In a similar way all the seeds collected at one time would be those that had ripened at approximately the same time. If seeds are crowded when they are planted, larger seeds will produce larger seedlings, which will have a better chance of survival. Larger seeds have proportionally more carbohydrate and less protein. The protein is in the embyonic area and is nearly the same irrespective of the size of the seed.

Why farm? Your students might wonder why, with those lush fields of wild einkorn, wheat was ever domesticated? If a family could supply its food needs for the year by a few weeks work, why not continue the wild harvest? One might suspect, however, that with such a natural bounty there would soon be a crowd of other Paleolithic folks to help enjoy it. One could argue, therefore, that the pressures of population size would lead to attempts to grow the cereals in places where they did not grow naturally, such as in the Mesopotamian lowlands where cities were to begin in a few thousand years.

There have been many speculative scenarios for the domestication of wheat and other food plants and almost no testable hypotheses. Harlan (1975, ch. 2) gives a fine overview and there are many important papers in Reed (1977). See also Harlan (1971), Harlan and Zohary (1966), E. Anderson (1952, ch. 9), Sauer (1952), Vavilov (1926, 1951) and de Candolle (1886).

Barley. In the earliest centuries of plant domestication in the Near East barley was more important than wheat. Cultivated barley, *Hordeum vulgare,* is derived from wild barley, *Hordeum spontaneum.* It is a grass, as is wheat. Wild populations of barley still grow abundantly in the hilly region of the Fertile Crescent (Harlan and Zohary, 1966). Barley is more tolerant of heat and is able to grow farther south than wild wheats. The details of its domestication are conjectural but we can suspect that, like einkorn and emmer, first the wild plants were used as food and later seeds were planted and protected by the first farmers.

Barley slowly became less important as human food and emmer wheat more so. Emmer was the preferred grain and when the ancient cities with their more stratified societies were founded, barley became the grain of the common man. Barley is still with us but today its importance for human beings is mainly for the production of beer.

Hooch. The use of fermented beverages is ancient and we may be sure that some barley was shunted from porridge production at a very early date. Some of our oldest written records, the Sumerian texts, mention 19 varieties of beer, a number equalled only in our better supermarkets today

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(Singer *et al.*, 1954, pp. 277–281). Although the fermentation of seeds and other plant materials may go back to the Paleolithic, there is no definite record (Jacquetta Hawkes, 1973, pp. 104–107). Nevertheless she suspects the worst (1963*a*, p. 317):

> There is no definite evidence for the fermentation of drinks in primary Neolithic societies, but as all mankind at every level from savagery to decadent civilization has always been dissatisfied with his state of consciousness and sought to change it by the use of alcoholic drinks (or other drugs), it is most unlikely that the first farmers were an exception. With a regular supply of grain, beer must have been brewed.

One does not have to credit some preinebriated genius with the discovery of fermentation. A stone bowl with some left over wild grain porridge would soon start to ferment, especially in warm weather.

Balacing the diet: pulses and pigs. The grasses that were domesticated in the Fertile Crescent—barley, einkorn, emmer—helped solve the constant ecological problem of obtaining sufficient food. Nevertheless, "man does not live by bread alone"; there must be other sources of protein. Although human beings have no trouble assembling amino acids into proteins, all animals must rely, almost exclusively, on green plants to make these starting compounds. The cereal grains (especially einkorn and emmer) have considerable protein but even better sources are to be found in the pulses—peas, beans, lentils. Still better sources for human beings are the proteins in eggs, milk, and the meat of pigs, chickens, sheep, goats, cattle, or other animals.

Proteins can be synthesized only if *all* of the component amino acids are present in sufficient quantities. One might look upon this as an extension of Liebig's Law of the Minimum—the amino acid present in minimum amounts will determine how much protein can be synthesized.

Milk and eggs are among the best sources for adequate amounts of essential amino acids. Plant proteins are often deficient in one or more amino acids. Long ago Osborne and Mendel determined this in some classical experiments with rats (see Boget *et al.*, 1973, pp. 87–88). Three experimental groups of rats were used. One group was fed protein from milk, another protein from wheat, and the third protein from corn. The group receiving milk protein remained healthy and grew rapidly. Those on wheat protein remained healthy but did not grow. Those on corn protein lost weight and eventually died.

The milk protein contained all of the essential amino acids required for health and normal growth. Analysis showed that the wheat protein did not supply sufficient lysine. When this was added to the diet, the rats grew normally. Corn protein was deficient in both lysine and tryptophan.

Human beings have the same problems making proteins as do rats. It is important, therefore, that many different sorts of food be eaten because that will give a better chance of obtaining not only the essential amino acids but also essential vitamins and minerals.

The diets of people who continued the hunter-gatherer mode of life until recent times were generally highly varied. The American Indians as a whole probably used at least 1,000 native plants (Yanovsky, 1936). Any one tribe would have had available far fewer but even the Chippewa of northwest Canada, with a relatively poor flora, regularly used about 38 native species (Densmore, 1928). The Aboriginals of Australia used about 400 species (Irvine, 1957).

Your students may be interested to discover how many of the foods they use are derived from plants. They will find that a relatively few species supply nearly all of the plant food they eat but, in addition, a huge number will be used in trace amounts (they might check the spice shelf and the list of contents on packages of prepared foods and drinks).

The Far East: roots and rice. At roughly the same time that the first domestications of plants were taking place in the Fertile Crescent, similar events were occurring in Southeast Asia. The archaeological data for Southeast Asia are not as good as they are for the Near East. Much less work has been done there and the climate is much less favorable for the preservation of artifacts

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and remains of food. Southeast Asia is part of the hot, humid tropics that extend in a belt around the world. The Fertile Crescent is temperate: much cooler, especially in winter, and it receives little rainfall.

Rice is the most important food plant contributed by the Southeast Asia area of domestication. Rice and wheat are the two main staples of the human population. One or the other can be grown in nearly every part of the world, except where it is very cold. Wheat is the crop of the cooler, drier, temperate regions. Rice is the crop of the warm, wet zone.

Although the evidence is incomplete, it appears that rice was not the first major plant species to be domesticated in Southeast Asia. Nevertheless, it was used as a food as early as about 6,500 years ago. Root crops, such as taro and yams, probably came first. Other domesticated plants from the area include various species of millet, beans, sugar cane, citrus, bananas, and breadfruit.

In the much cooler and drier areas to the north, in central China, other species of millet, soybeans, apricots, peaches, cucumbers, and Chinese cabbage seem to have originated. Rice was in cultivation at least as early as 5000–4500 B.C. As always, the species first cultivated were the wild plants gleaned by the gatherers. Wheat and barley appear early but their origin is not known. Presumably they were introduced from the Near East.

Here is a puzzle for your students. Rice, taro, and yams are grown extensively throughout Southeast Asia today. The islands of the South Pacific are believed to have been settled by people from Southeast Asia. When European explorers first reached the islands they found the natives growing taro and yams but not rice. Later rice was introduced and became the main food plant. How can one account for the absence of rice until recently?

A commonly accepted explanation is that taro and yams were domesticated earlier than rice in Southeast Asia and that it was during this early period that the migrations of human beings to the islands took place. Later their friends back home began to domesticate rice (see Gorman, 1977).

Sub-Saharan Africa. Africa south of the Sahara Desert was discovered by Europeans at about the same time they came to the New World. This surprisingly late date was a consequence of their limited abilities at sea and, on land, the Sahara desert was an almost imprenetrable barrier. Exploration by sea began in the 15th century when Bartholomew Diaz reached the Cape of Good Hope in 1488 and Vasco da Gama rounded the Cape and sailed all the way to India in 1497–1499. The difficult terrain, oppressive climate, and unfriendly organisms (big and small) retarded the rate of discovery.

During the long ages that the rest of the world had been isolated from Africa, the native Africans had developed an extensive agriculture. Once again, grasses were important articles of diet: several species of millet, sorghum, and a species of rice different from that of Southeast Asia. There were pulses—peas and beans—that supplemented the scanty protein of the cereals. Other important plants of African origin are coffee and watermelon.

The New World: Irish potatoes and Indian corn. European explorers found the native Americans cultivating a variety of extremely valuable food plants. Many quickly assumed worldwide importance. The more notable species on the New World list are Indian corn (or maize), the lima and common bean, sweet potato, manioc, potato, peanut, pineapple, tomato, squash, and tobacco.

Indian corn, *Zea mays*, is the third most important human food, following rice and wheat. Its biology is fascinating. It grows in more diverse habitats than any other cereal: in the temperate zones and the tropics; in semiarid regions and rain forests. This is not a consequence of a single genetic type being able to tolerate such diverse habitats but rather the evolution of the species into hundreds of different races, each adapted to a specific soil and climate. The ancestor of corn is the wild grass, teosinte (*Euchlaena mexicana* or *Zea mexicana*).

Corn is the principal food in Mexico and Central America. When combined with beans it provides a nutritious diet. Corn is deficient in the amino acids lysine and tryptophan and in niacin, a vitamin for which tryptophan is a precursor. The Pre-Colum-

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bian Americans developed a way of preparing corn that greatly improves its nutritional qualities. The dried corn is treated with hot water containing about 5 percent lime. It is then ground and made into tortillas. About two-thirds of the lysine of untreated corn is in the glutelin fraction, which is almost indigestible. The lime treatment serves to free the lysine.

Lack of niacin (for which tryptophan is a precursor) leads to pellagra. This deficiency disease causes dermatitis, diarrhea, depression, confusion, and hallucinations. It is widespread in populations that subsist largely on corn not treated with lime.

Pellagra was common during the years of the Great Depression in the southeastern United States, where the corn was not treated with lime. Pellagra is caused not only by inadequate amounts of tryptophan but also by inadequate amounts of isoleucine relative to leucine. Thus an increase of the isoleucine to leucine ratio will be beneficial. The lime treatment increases the ratio by 1.8 times. Although the lime treatment has the overall effect of reducing the amino acids, except for lysine, it greatly improves their ratios and hence makes the food more nutritious. Pellagra is a rare disease where the corn is treated with lime before it is consumed.

When the Spaniards under Pizarro entered the empire of the Incas they found that the most important food plant was the potato, *Solanum tuberosum*. It had been cultivated for at least two millennia and possibly much longer. The potato is thought to have beem domesticated in the Bolivia-Peru region of the Andes, possibly near Lake Titicaca. There are many wild species with varying numbers of chromosomes. The commonly cultivated varieties are tetraploid.

The wild species of potatoes often have considerable concentrations of alkaloids, which makes them bitter and poisonous. One of the early steps in domestication must have been the selection of varieties with less alkaloid. Even the potatoes we eat, if allowed to be in strong light for a long time, develop an alkaloid—solanine. Since the exposure to light will also cause the tubers to become green, due to chlorophyll, one can avoid solanine by avoiding green potatoes.

The potato was introduced into Europe in the 16th century, and, in a very short time, became a major food crop for people in the cooler parts of Europe. It is rich in carbohydrate and the protein, though modest in quantity, is excellent in quality. The potato was introduced to the United States from Europe, not from its home in South America.

The tropical root crop manioc, or cassava (*Manihot esculenta*), was one of the most important sources of food for the original inhabitants of the wet lowlands of South America. That it could be used at all tells us a very great deal about those first cultivators of at least several thousand years ago (Harris, 1972, 1977; Purseglove, 1974, pp. 171–180). Manioc contains a deadly poison, hydrocyanic acid (HCN). The HCN is liberated from the glucoside linamarin by the enzyme linase. When the plant is growing the enzyme is nearly inactive. When the tubers are dug and begin to wither, the enzyme becomes active and HCN is produced. There are many varieties of manioc and the amounts of HCN vary. For example, the sweet maniocs have low concentrations of the poison, which is localized in the skin. The tubers, however, become edible when they are cooked and peeled. The bitter maniocs are more poisonous and the hydrocyanic acid occurs throughout the tuber. The solution here was to peel the manioc, grind it, and then to place it in closely woven baskets, which were squeezed to expel the liquid with the poison. Then it was cooked. The same process used in prehistoric times is used today, and one of the products is tapioca.

The Neolithic accomplishment: plants

The plants and animals that now supply our need for food, fiber, and transportation were all brought into domestication before the end of the Neolithic. We can accept that this accomplishment required important problems of human ecology to be solved. The main events that occurred were the slow adaptation of the various

species to new climatic regions as they were carried from their places of origin. This involved genetic selection which, more often than not, was probably incidental to farming. Obviously, only those plants that could survive the new conditions would become the progenitors of the next crop. It is not known when deliberate selection became a powerful tool of plant improvement, as it has been in recent centuries.

There were four essentially independent areas where considerable domestication of plants occurred: the Near East, Southeast Asia, Sub-Saharan Africa, and the Americas. In each area the local wild plants that had served the hunter-gatherers were the species domesticated, yet there are astonishing parallels. Each has one or more important grasses: wheat and barley in the Near East; rice in Southeast Asia; millet and sorghum in Africa; corn in the Americas. Each has several pulses—peas and beans of many species—that add vital protein. Each has its root crops: turnips, radishes, carrots, and beet in the Near East; taro and yams in Southeast Asia; several other species of yams in Africa; sweet potatoes and the Irish potato in the Americas. Thus, a similar diet was possible for human beings throughout the world (except for the Arctic where human beings are essentially carnivores).

Seeds of grasses are the plant foods that still form the major fraction of the human diet. They can be produced in vast quantities and supply the purely caloric needs. When supplemented with pulses or a little meat a complete diet can be attained. A hunter's food must be eaten promptly lest it decay (although it can be preserved by drying in some cases). The seeds of grasses and the pulses can be stored for months or, with care, for years. Cultivation of plants can produce a crop that can be two orders of magnitude greater than a hunter-gatherer could secure from an area the same size.

Human beings have other uses for plants. Some have been cultivated for their fiber: flax (Near East); various species of cotton (Africa, Asia, the Americas); several species of hemp (Asia); jute (southern Asia); sisal and other *Agave* fibers (the Americas). Innumerable species are used by recently studied hunter-gatherers for medicine, dyes, poisons, pleasure, and tools.

Taming the wild beasts. The details of domestication of animals are not known but it is highly probable that it began when young animals were captured and raised as pets. Dogs appear to have been domesticated from different species of wild canines in different parts of the world. They were probably the first mammals domesticated, and alone among all domesticated animals, were on all continents. One pleasant theory is that man and dog began their long association as hunting companions. If so, domestication probably first occurred when human populations were in the Paleolithic hunter-gatherer stage. Asia, and especially western Asia, contributed most of the animals used for food and as beasts of burden: cattle, goats, pigs, sheep, chickens, donkeys, camels, horses, and the reindeer. The New World provided very few domesticated animals: turkey, llama, alpaca, and guinea pig. Africa, with the most abundant fauna of large mammals of any continent, gave us the ass.

Fibers for clothing and other products are provided by sheep, goats, the alpaca, and the camel.

The horse was an important food source during the Ice Age and was probably domesticated for that purpose—somewhere in the vast grasslands of Eurasia. Later it carried warriors of the Near East into battle and carried produce from farm to village. Elephants and water buffalo became beasts of burden in southern Asia. The llama and in some instances the dog were used for transportation in the Americas. See Clutton-Brock (1981), Herre and Rohrs (1977), Ucko and Dimbleby (1969), Zeuner (1963), Angress and Reed (1962), and Reed (1959).

Tools and household implements. Tools were made of stone, bone, wood, and shells—metal was still in the future. Pottery had appeared about 9,000 years ago and by the end of the Neolithic it had been moulded into an incredible variety of pots, vases, containers, and objects with many func-

tions. Baskets and mats were woven from fibrous plant material at hand. As mentioned before, some baskets were so closely woven that they could be used to hold water and, so, to cook food by boiling. Houses were made from the materials at hand: stone and adobe in the dry areas of the Near East; logs where trees were abundant; bamboo and thatch in the tropics; tents of skin served the nomads.

A summing up: the Golden Age?

The pre-agricultural millennia, roughly equal to the Paleolithic and Pleistocene, account for about 99 percent of the time our lineage has been in the human stage. Some authors have looked upon that time as the true Golden Age of our species. It is pointed out that the hunter-gatherers of recent times have an easy life that demands only a few hours each day for subsistence activities and it is assumed that the same state of bliss characterized the Paleolithic.

> The ethnographic evidence indicates that people who do not farm do about everything that farmers do, but they do not work as hard . . . . There is evidence that the diet of gathering peoples was better than that of cultivators, that starvation was rare, and their health status was generally superior, and that there was a lower incidence of chronic disease . . . . Why give up the 20 hour week and the fun of hunting in order to toil in the sun? . . . Why abandon the Golden Age and take up the burden? (Harlan, 1975, pp. 31–32).

But this argument would seem to imply that every wild species is in a Golden Age. There are reasons to think, however, that the Paleolithic may not have been such a Garden of Eden. During much of the time hunter-gatherers may secure the necessities of life but, sooner or later, the times of trouble and sorrow will come. Drought and unfavorable conditions will reduce the harvest of wild seeds and roots and the wild animals hunted for food. Liebig's Law of the Minimum applies here as well. The size and well being of the human population depends not on the good years but on the bad years.

Natural populations, and we must include human beings in the Paleolithic, are controlled more by external than by internal factors. The potential in each species for increasing the size of its population is such that, if unchecked, the earth would soon be filled. Nevertheless, the actual rate of increase of the human population during the Paleolithic was, as we have noted before, close to zero. Yet the imperceptibly slight positive rate was sufficient, over the vast expanse of more than a million years, to bring the human population to an estimated 5–10 million. Harrison Brown (1954, p. 14) estimates that "the earth probably could never support a human population of more than about 10 million depending upon hunting and wild vegetation." Schwanitz (1966, p. 1) estimates that if the human population was "dependent on hunting and foraging as the only source of food, the earth could not support more than 30 million people." Today the earth supports more than a hundred times as many.

So by the end of the Paleolithic the earth may have been reaching its carrying capacity for human beings and the inexorable pressures of a slowly increasing population size would have put a selective advantage on the invention of techniques that would increase the available resources. Thus, there were pressures to abandon this Paleolithic Garden of Eden (even if it ever were such) and to enter the Neolithic when, henceforth, more food could be obtained, but by the sweat of the brow.

The causal relation between population pressure and the development of agriculture is uncertain. Some anthropologists believe there is a link. For example Cohen argues (1977, p. 279) that,

> hunting and gathering populations had saturated the world approximately 10,000 years ago and had exhausted all possible (or palatable) strategies for increasing their food supply within the constraints of the hunting-gathering lifestyle. The only possible reaction to further growth in population, worldwide, was to begin artificial augmentation of the food supply.

Murdock (1967) and Hassan (1981) sup-

port a similar hypothesis. Other anthropologists point out that some hunter-gatherers had high population densities without agriculture, for example, the Aleuts with their rich fishing grounds in the Bering Sea. We can accept, I believe, that some rich source of food would be necessary for dense human populations. This could have come from marine resources or when agriculture was well established.

The die is cast

So we come to a watershed in the human drama. The human population is subject to the same ecological constraints that apply to all organisms—the ability to obtain resources. Tools, fire, and the cultivation of food all have the inevitable consequence of providing more resources for the human population and hence increasing the probability of reproduction by its individual members.

Thus, the ecological consequence of our cultural evolution is to make more resources available, which will allow more individuals to reproduce, which will require ever more resources, which will allow still more people to reproduce, which will . . . .

Such a process can continue only so long as there are infinite resources. Yet the drama of human life is being played out on a finite earth. There is built-in tragedy and built-in promise. Which dominates can be a matter of human choice.

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More and more people: the tradeoffs

Civilization is based on cities, as the etymology of the word implies. The city was the home of the citizen whose civility contrasted with the manners and behavior of the barbarian and the rustic. To this day the cities remain the center of the arts, industry, and the political and social life of nations. This is a consequence of a very large number of human beings living close enough to interact with one another.

The ecological problems that emerged when human beings first began to form cities were immense—and many are still with us. As is the case with most topics, students will gain much if they first try to list the special ecological problems that they believe to be inevitable when large numbers of individuals live in a small space.

The settled life of the early Neolithic farmers was based on small villages. They were small for good, practical reasons. With primitive methods of farming, a village of 150 inhabitants would require about 1,600 hectares (4,000 acres), depending on soil and climate, to raise the necessary food. How far would the individual who farmed the most remote plot have to carry the tools and produce from and to the village? Your students could determine this for themselves. The most ideal situation would be for the farm land to form a circle around

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the village. If that was so the circumference would be about 2 kilometers distant. If the population was 1,500, the journey would be about 7 kilometers. For a population of 15,000 the farmer would have to travel about 22 kilometers.

Walking to and from the village would waste both time and energy that could be devoted to food production, making tools, household tasks, or enjoying life. Thus, there are practical limits to the size of a farming village. The size can be larger if the land is fertile but it must be smaller if the land is poor. If transportation is available, more distant fields can be farmed. In Neolithic times the principal means of transportation in the Near East, apart from walking, was the donkey, which could be counted on to carry a moderate burden at a speed of about five kilometers per hour. Crude boats were available but the places where they could be used were rare.

A settled community would need to have a reliable and convenient source of water. The size of the source would limit the size of the community. There would also have to be a renewable source of a fuel such as woods, reeds, or dung. And again, the amount available would limit the size of the community.

The interactions that are possible within a community can lead to better and more varied lives for all individuals. The time came when each farming family could produce more food than it required for itself. The resulting surplus could be used to support other individuals who could become specialists: leaders, potters, weavers, carpenters, merchants, miners, warriors, masons, jewelers, physicians, sailors, servants, architects, teachers, priests, astronomers, and scribes.

The Neolithic communities brought from Paleolithic times the social system of hierarchies of authority, initially based on strength. The father of the family was its head. The strongest and most effective member of a band of nomads became its chief. Later, as the communities grew, came the generals and kings. There has never been a time in history without rulers of communities, whatever their size. There are valid reasons for this arrangement. Communities are effective to the degree that they can obtain the resources for life and protect the members of the community from adverse forces from within and without. Effective communities are of great ecological importance because they increase the chances of survival and reproduction of the individuals in the community.

The division of labor within the hierarchical social structure of the community was the key development for the very rapid cultural advances that began with cities. It also became an increasingly important contrivance for dealing effectively with the environment.

But there were, and still are, negative ecological tradeoffs. The larger the human community, the more severe are the pressures on the adjacent biological community. Natural habitats are replaced and, in so doing, there will be destruction of that portion of the biosphere. The larger the area destroyed, the more serious will be the consequences for the human population.

The destruction of the native flora and its replacement with cultivated plants will almost always increase soil erosion. This is especially true in areas with marginal amounts of rainfall—as is the case in most of the Near East. Erosion carries off the topsoil, laboriously built up by living organisms over the ages. Topsoil is, of course, essential for plants and so indirectly for animals.

The domesticated animals associated with settled communities are important as a source of food, fiber, and work but they too contribute to the destruction of the environment. Grazing animals, especially sheep and goats without sufficient pasture, reduce or even destroy the plant cover thus exposing the surface to severe erosion.

Farming damages the soil in still another way. In a natural habitat the plants die *in situ* and the minerals they contain are recycled by other organisms. But when crops are removed from a field, so are the essential elements they contain.

Thus we must accept that the fertility of the soil will influence the life of all organisms. In a natural environment, the fertility

is maintained by the activity of the organisms themselves. If this fertility is lessened by cropping, grazing, and the destruction of the local biota it must be improved by adding fertilizer or allowing the land to lie fallow, which permits natural processes to increase fertility.

When human communities reach sizes that exceed the carrying capacity of the land being utilized, environmental damage is inevitable. Thus, the very basis for human life is eroded and the same area can now support only ever smaller numbers of human beings—it has become overpopulated.

The ancient solutions were to reduce population size by the migration of the excess population, to increase the area of land in use, and to develop means of transportation so that distant lands could be tapped, or to attempt artificial population control. If none of these solutions was effective nature took over and there was starvation. A population totally dependent on a limited area of land cannot exceed the carrying capacity of that land.

Another negative tradeoff was that, as communities increased in size, so did intercommunity competition, and hence aggression and war. Large communities can field large armies for defense or offense. In ancient times, warfare tended to be a winner-take-all affair. The inhabitants of the vanquished community were "put to the sword" or taken as slaves and their community "put to the torch."

It is probable that intragroup violence and crime increased as well, as communities got larger. Let us assume that for whatever reason about one percent of the individuals were criminals. A community of 150 might be able to deal effectively with one or two "bad" individuals. A community of 1,500 would have a gang of 15 and for a community of 15,000 there would be 150. Thus, as the communities grew so would the absolute numbers of their difficult citizens, whose effectiveness would increase with their group size, unless measures of control existed.

Another negative tradeoff of increasing size is the increase in disease. The native peoples of recent times that lived in small and semi-isolated groups were relatively free from contagious diseases. Either the disease organisms never reached them or, if they did, there were not enough human beings to keep the disease going.

Thus it is now known that it requires a population size of at least half a million for the virus responsible for measles to be maintained (W. H. McNeill, 1976, p. 53). McNeill concludes that "Person to person 'civilized' types of infectious disease could not have established themselves much before 3000 B.C." As communities grow and communication between them increases, contagious disease organisms are able to spread more rapidly and to establish themselves in the population.

In time the inhabitants of larger communities will develop some degree of immunity to those diseases which they have encountered. Inhabitants of isolated or rural areas will have little immunity. This can have devastating consequences for the populations lacking immunity. European settlers carried their diseases, for which they had considerable immunity, throughout the world and transmitted them to peoples with little or no immunity. Thus a disease "mild" to Europeans brought death to the natives of America and the South Pacific.

And then there is the problem of getting rid of human wastes. It could be relatively easy to walk to the edge of a small village to dispose of decaying food, urine, or feces if an inhabitant was so inclined. Such disposal would have important public health benefits and could enrich the fields. However, as villages grew into cities, the problems would become greatly exacerbated—it would be just too much trouble to walk that far.

These wastes become a serious problem if they contaminate the community's water supply or food. Amoebic dysentery and various other diarrheal diseases, typhoid, and numerous protozoan and helminth parasites are transmitted from person to person in contaminated food and water. The larger the community the larger the quantity of wastes and the greater the probability of contamination. We have no firm data for Neolithic communities but,

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since pronounced improvements in public health are rather recent, these 1841 data for two areas in England are suggestive. the expected life span of males in the smoky industrial city of Manchester, with no sewers, was 24 years whereas for males in rural Surrey it was 44 years (D. V. Glass, 1964).

So the concentration of human beings that was to make civilization possible introduced serious ecological problems. But in human biological terms the benefits may outweigh the costs. Numbers spell power; and from the later centuries of the Neolithic to this day, cultural advances have come largely from cities.

From the Paleolithic on, human beings began to replace a high degree of biological independence with increasing interdependence. Most individuals in the Paleolithic could secure the basic necessities of life by their own efforts. This was still true in the first half of the Neolithic but thereafter this became impossible for an increasing proportion of human beings—mainly those living in the larger communities. The increasing interdependence was to lead to a new sort of freedom for some, however. This was a freedom to participate in what we would now call the arts, sciences, rituals, government, and intellectual activities in general.

"History begins at Sumer"

Or so it is claimed by Samuel Noah Kramer in his book with this title. There are no data to refute his assertion. Ancient Sumeria is situated in the lower part of the Valley of the Twin Rivers, the Tigris and Euphrates in what is now southern Iraq. Both rivers begin in the mountains of Armenia and flow south through the Fertile Crescent and the plains of Mesopotamia. The rivers carry a heavy load of rich alluvium that over the centuries has produced the broad flood plain. The rivers unite to form the short Shatt-al-Arab (now the site of the war between Iran and Iraq), which enters the Persian Gulf.

Here lying buried in the desert sands are the remains of the first civilization and the first cities: Eridu, Uruk, Lagash, and Ur (the original home of Abraham, Genesis 11:26ff). The land near the rivers where these cities were located was a combination of marsh and of desert. The rainfall was insufficient for agriculture.

The first systematic archaeological excavations of the cities of Sumeria, mainly of Ur, that were to tell us of the early inhabitants, were done in the 1920s by a joint expedition of the University of Pennsylvania and the British Museum led by Sir Leonard Woolley (Woolley *et al.*, 1927–1956). The extraordinary monuments and artifacts discovered bespoke of a high culture in what were the first cities of the human race. There were monumental buildings made of sun-baked bricks of mud and reeds; there was no local stone or wood for construction.

The Sumerians were the first to invent writing. This began as ideograms and evolved into a mixture of ideograms and phonemes. The ability to keep written records, plus a knowledge of simple mathematics, allowed the priest-administrators and merchants to keep track of people, produce, and transactions. There was an elaborate priesthood with the chief priest the king. The elite demanded and received the excess wealth of society and organized the masses to erect palaces, city walls, ziggurats with their crowning temples, and to form armies. The elite went to their graves accompanied by jewels, fine weapons, and other belongings. Bronze was used mainly for weapons; the farmers continued to use stone, wood (imported), and bone for their tools.

Woolley estimates (1963, p. 428) that, at its height, the population of Ur was an astonishing 360,000. It is interesting to enquire how one can estimate the population of a city of about 4,000 years ago. The excavations showed that there were about 44 houses per acre. Most of these were of two stories and a conservative estimate would have placed about 6 persons, including slaves, in each household. The built-up portion of Ur occupied about 1,450 acres. That would give a total population of about 382,800 so, by reducing this for open spaces, we arrive at Sir Leonard's estimate. Some more recent estimates are lower since it is suspected that not all of the area of the city might have been occupied at the same time.

Nothing like the civilization of Ur was

known from earlier periods, producing the impression that a single leap took our ancestors from barbarism to civilization. But that impression must be wrong. The separate cultural innovations that were to make cities and civilization possible must have come first. Human beings could not assemble in a city and become civilized. They had to develop the basic requirements of civilization in order to form cities. This period of preadaptation was probably completed early in the fourth millennium B.C. (possibly about 3800) in the city-states of Sumeria.

Cultural evolution was so rapid in the fourth millennium that some historians speak of the "Urban Revolution" that took place in Sumeria. But surely it must have been an "Urban Evolution." The welding of a large mass of human beings into an organized society requires a long cultural preparation. There must be that ability of farmers and herders to produce a surplus of food to support those not so engaged. There must be effective leadership and disciplined followers. Once organized in cities, human cultural evolution was rapid. But Jacquetta Hawkes (1973, p. 4) reminds us that something more is needed:

> Good soil, agriculture, some elementary techology, social stratification may have made the necessary groundwork, but what except imaginative power lifted inert mud into the fantastic ziggurat with its crowning temple, or the resistant mass of rock into a gleaming pyramid?

The land was so bleak and inhospitable that ancient Sumeria was essentially uninhabited until about 5000 B.C. The photograph on page 78 of Kramer (1957) shows the region now as a barren desert and it is highly probable that it was the same before the first people arrived. Rain-dependent agriculture was impossible; the desert summers were blistering and the winters cold; the erratic rivers were subject to serious and frequent flooding and changes of course. But people came, probably from the highlands of Iran to the east. The fact that they did migrate to such a harsh region probably meant that population pressures in their homeland required the move. They brought their domesticated animals and plants (except the olive) and acquired a new one—the date palm (*Phoenix dactylifera*). An important genetic event had occurred with respect to barley. The first barley to be domesticated had two rows of seeds in the head. A new form, with six rows of seeds, is recorded from the earliest Sumerian times. This must have been a chance mutation that was preserved because it gave far more food.

Irrigation

Apparently these immigrants from the east were responsible for the first large scale conversion of barren desert to agricultural land by irrigation. During a thousand years or so they extended canals from the rivers to essentially all of the southern part of the valley. The highly fertile alluvial soil, when watered, began to produce large amounts of food, and so made possible a very large human population (Figs. 3–5).

The relatively gentle (except at flood time) Euphrates, rather than the turbulent Tigris, became the source of water for irrigation. The geography of the region made irrigation farming possible at first but ultimately impossible. The Euphrates is a rapidly-flowing, silt-laden river until it reaches the almost perfectly flat plain of southern Iraq. There it slows and deposits its silt mainly along the banks (where the flow would be the slowest). This elevates the banks, which become natural dykes and the crest of the river becomes higher than the surrounding plain. This makes it a simple task to irrigate the fields. The bank can be cut and the water carried by gravity through the canals across the plain. Thus in this land of almost no rain the potentially rich soil can be irrigated to produce an abundant harvest.

But it is not this simple. Successful irrigation demands not only a supply of water but, just as important, a mechanism for getting rid of salt. The principle is easy to demonstrate. If one places water from almost any natural source in a container, leaves it in the sun, and continually replaces the water that evaporates, soon the water in the container becomes very salty. Thus, when the waters of the Euphrates, which carry an appreciable amount of salt, were allowed to flow over the land year after

FIG. 3. Tilling the soil in northern Mesopotamia (now Iraq) about 1901. Similar tools began to be used in the early Neolithic. Keystone-Mast Collection of the California Museum of Photography.

year, the salt left in the soil reached levels that made farming impossible.

Ideally, irrigation is a flow-through process. Water is carried to the fields but the amount is so regulated that some is left to flush the soil and carry off the excess salt. The land in Sumeria is so flat, however, that drainage is a difficult problem. The water cannot flow directly back into the river, which is higher than the plain.

Even apart from this difficulty, irrigation was not easy. The erratic nature of flooding by the Euphrates made it difficult to maintain the irrigation canals and even the natural banks of the river. As a consequence, a large proportion of the total human energy was devoted to maintaining the canals: first digging canals many miles in length; maintaining their banks, especially during flood time; and clearing them of silt. A task of this magnitude could be accomplished only by a very large number of human beings who were either forced or persuaded to do it. According to Sir Leonard Woolley (1963, p. 419),

> The Mesopotamian delta held out to early man the promise of a better and

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FIG. 4. Threshing beans in Egypt about 1909. The threshing sledge is an ancient device used for freeing seeds from their seed coats, pods, etc. Keystone-Mast Collection of the California Museum of Photography.

richer life than could be found in any neighbouring land, but it was a conditional promise; its fulfilment required a co-operative effort and a centralization of control quite beyond the scope of a village community. The very nature of the country and of the river forced the inhabitants to make common cause throughout a territory whose size was decided by the limits of an interdependent canalization, and the planning and upkeep of the canals required the direction of a regional authority enjoying absolute powers.

The task of maintaining the irrigation canals was made more difficult by the all too frequent wars. Canals were deliberately destroyed and, of course, if the peasants had been drafted for the army they were not available for repairing and maintaining the irrigation system. Then there were the natural disasters—when the rivers flooded far above normal and washed out canals and banks.

But in the long run disaster came as a consequence of faulty agricultural practices that led to excessive salinization of the soil. Jacobsen and Adams (1958) tell the

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FIG. 5. Grinding grain. The seeds of wheat, corn, other cereals, pulses, and nuts are usually ground to form flour or meal before being eaten. Until recently this was done by crushing the grain with stones. Simple grinding stones, such as that shown in the left photograph, were used by the Native Americans (this one in

story. See also Adams (1965, 1974), Gibson (1974), Lawton and Wilke (1979), Pillsbury (1981), and Whyte (1961).

In the absence of proper flushing, the water table of irrigated lands becomes highly saline. This need not be disastrous *if* the upper level of the water table is below the roots of the crop plants (the cereals have very short roots). There are two ways to keep the water table low. One is to use a minimum amount of water for irrigation. This will prevent the soil from becoming saturated down to the water table, allowing the salty water to move upward through the moist soil to the roots. The second method is to allow the fields to lie fallow every other year. This allows the growth of salt tolerant native plants with deep roots. These plants will remove water from the soil above the water table and the drier soil acts as a barrier to prevent salty water reaching the roots of the crop plants.

But the Sumerians were not able to prevent the increase in salt and slowly the land became less productive. This can be shown by comparing the relative percentages of wheat and barley grown. Wheat is more sensitive than barley to salt. It is possible to obtain rough estimates of the grains being used for food by studying the bottoms of clay pots dug up by the archaeologists. Before the pots were fired, they were often put on the floor of huts and the seeds lying there made impressions in their soft clay bottoms.

Using this method Jacobsen and Adams reported that barley and wheat were equally abundant around 3500 B.C. By 2500 B.C. wheat had dropped to about 16 percent and by 2100 B.C. to 2 percent and

southern California). Similar devices were used in many parts of the world. A more advanced way of grinding grain between stones is shown in the right photograph (Manchuria about 1904; Keystone-Mast Collection, California Museum of Photography). The donkey's eyes are covered to prevent dizziness.

by 1700 B.C. there was no evidence that it was used. Since wheat is the preferred cereal, we can conclude that it was not grown because the land was too salty. The yields of grains, known from ancient records, also showed a drop. About 2400 B.C. farmers in one locality harvested an average of 2,527 liters of grain per hectare. The average declined to 1,460 liters in 2100 B.C. and 897 liters by 1700 B.C.—a yield approximately one-third of that 300 years before.

By 1700 B.C. the great cities of Sumeria had declined to impoverished villages or were totally abandoned. Salinization was not the only cause. The human predilection for violence and war resulted in frequent episodes of destruction of these communities and the disruption of their systems of irrigation. But recovery was always possible when there was that cadre of peasants who could produce that large surplus of food that supplied the cities. This became impossible when that basis of all life, the fertility of the soil, had been destroyed.

The most awesome aspect of all is that the land is abandoned to this day.

The human population had experienced one of its first major ecological disasters. That was not the end of civilization, of course, but it was the end of civilization in Sumeria. Civilization moved elsewhere, yet the scenario of environmental destruction followed by the decline of civilization was to be repeated again and again. The combination of vast concentrations of people and an ever more powerful technology inevitably demands more resources than the environment can supply. All civilizations, not just the cities of Sumeria, depend

on the surplus production of renewable resources and the availability of nonrenewable resources.

The Indus River civilization

About five centuries after civilization began in Sumeria, another center arose quite suddenly in the Valley of the Indus River, in what is now Pakistan. Much less is known about it yet its demise appears to be another example of the human destruction of the environment.

This civilization is known as the Harappan civilization from one of its main archaeological sites on a tributary of the Indus River. The Indus is a large river that flooded each year and so renewed the fertility of the land. (The Indus rises in the Himalayas and enters the Indian Ocean near the present day city of Karachi.)

The Indus cities probably began about 2500 B.C. The major sites so far studied are Harappa, far upstream, and Mohenjodaro, about 200 kilometers from the Indian Ocean. There was a well-developed agriculture based on wheat, barley, and peas. Cotton was grown and woven for clothing. Sheep, pigs, cattle, water buffalo, camels, horses, cats, dogs, and possibly elephants had been domesticated.

The Harappan civilization reached a peak about 2350 B.C. and lasted until about 1600 B.C. One prominent hypothesis for the decline is that the forests along the river were destroyed (for fuel) to such an extent that the land was seriously eroded and subject to devastating flooding by the river.

How would one come to such an hypothesis? The evidence that there were forests is that archaeologists find remains of animals that are forest dwellers: tigers, elephants, water buffalo, monkeys, and rhinoceros. That forests existed and were destroyed is suggested also by the fact that the cities were built of fired bricks. These were needed in vast quantities and trees were the only source of fuel that could have been used for heating the kilns in which they were made.

There were other factors, of course: invading armies did their periodic mischief. It must be remembered, however, that violent destruction need not mean the end of a city. Some of the ancient cities of the Near East and the Mediterranean world were repeatedly sacked, yet they are still with us (Rome and Istanbul, for example). If a city has a viable ecological basis for its existence it may "rise again from its ashes."

Ancient Egypt

The third of the great civilizations of antiquity began in the Valley of the Nile. This is a happier story because, to a large degree, the ancient Egyptians lived with a river that made their soil a constantly renewed resource. The soil's fertility that was removed with each harvest was restored by the Nile's flooding the following season. When the water receded it carried off any excess salt. This ecologically benign arrangement lasted for more than five thousand years and only in our time has it been abrogated—by the Aswan High Dam (completed in 1970).

The Nile is one of the great rivers of our world. Its ecological importance in human terms is that it made life possible in the Nile Valley, which beyond the banks of the river is a desert where it almost never rains. Its importance for the study of history lies in the fact that European scholars began to study the ancient monuments along its banks long before they started digging in Mesopotamia. Thus Egypt came to be regarded as the world's oldest civilization. It nearly was—the Sumerian cities seem to have come into existence only a few centuries before civilization started in Egypt. Sumeria lasted only about two millennia—Egypt is still with us—and the reasons are largely ecological.

The first large scale study of Egyptian antiquities was made by the savants accompanying Napoleon on his ill-fated (for him) attempt to conquer Egypt. They studied the monuments, made splendid paintings of them, discovered the Rosetta Stone that proved to be the key to deciphering the ancient hieroglyphs, and published 21 magnificent volumes (Description de l'Égypte, 1809–1828) describing what they had found.

The Nile floods are the result of heavy rains in the headwaters of the river in

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Ethiopia and, to a lesser degree in the Lake Region of East Africa. Scholars of ancient times did not know this and were sorely perplexed by the behavior of the Nile. It flooded from July to October when all the other rivers they knew about were at their lowest levels. This vast river appeared to rise in the desert far to the south, a desert beyond which was terra incognita. In Victorian times there was a frenzy to be the first to solve the problem—the source of the Nile. British explorers endured great hardships of distance and disease before they found the answers (Moorehead, 1960, part 1; 1962, part 1; Burton, 1860; S. Baker, 1866, 1867; Bruce, 1790; Speke, 1864).

The Nile has two main tributaries. The shorter Blue Nile begins in the mountains of Ethiopia and, because of its greater drop causes more erosion and, therefore, carries vast amounts of silt. The White Nile rises from lakes of East Africa. Its more gentle flow and passage through a hugh sieve of a marsh (the Sudd) means it carries less silt than the Blue Nile. The two tributaries join at Khartoum and the river, a ribbon of life, continues north for 2,500 kilometers before it enters the Mediterranean. It has a huge delta with exceptionally fertile soil and, today, a dense population of exceptionally impoverished inhabitants.

The Nile thus behaves very differently from the Tigris and the Euphrates. Most importantly, it is fairly reliable. In contrast to the turbulence and variations of flow of the other rivers, the Nile begins to flood slowly in July and spreads across its low banks to the plain on either side. The shallow waters are slowed and they deposit their rich silt from Ethiopia. Then slowly the level of the river drops and the waters drain back to the main channel. Recall that this is impossible in Sumeria because the Euphrates is higher than the surrounding plain. Furthermore, the slope of the land in the downstream direction of the Nile is about twice as great as is the slope of the plains of Sumeria. Irrigation therefore is a flow-through process, which reduces the risk of salinization.

The original system of Egyptian agriculture was a single crop per year using the natural irrigation of the Nile floods. When the fields began to dry in November they were planted with wheat, barley, onions, beans, lettuce, melons, and leeks. The rich soil produced abundantly. In addition, grapes and fruit trees were grown. These had to be watered throughout the year artificially as did the kitchen gardens.

But the inevitable happened. The population increased, though slowly, and soon the harvest of a single planting per year was insufficient. It became necessary to irrigate the fields so that two or more crops could be grown each year, but the population continued to expand and somehow the supply of food never seemed to be sufficient.

At this point we will consider some aspects of poulation growth and the factors that limit it, mainly starvation, disease, and intraspecific violence. Then we will return to our consideration of the ecological problems that have confronted the human population in Egypt and elsewhere over the centuries.

References to cities and the beginnings of civilization

General references. R. M. Adams (1960), R. M. Adams *et al.* (1968), Albright (1954), Bottero *et al.* (1967), Boyden (1970), Braidwood and Willey (1977), Brothwell (1969), Carter and Dale (1974), Childe (1942, 1957), G. Clark (1969), Coon (1958), Darlington (1969), Diringer (1962), Eckholm (1976, ch. 7), Edwards *et al.* (1970–1975), Fenner (1970), Frankfort *et al.* (1946), Hawkes (1963*b*, *1973), Hodges (1971), J. D. Hughes (1975), E. Jones (1966), McEvedy (1967), *McNeill (1963), Maddin *et al.* (1977), Marshack (1972), Michener (1965), Moorey (1979), Neugebauer (1952), Postgate (1977), Pritchard (1958, 1975), Roebuck (1966), Scientific American (1976), Singer *et al.* (1954), Ucko, Tringham, and Dimbleby (1972), and *Woolley (1963).

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References to the Indus River civilization. Fairservis (1975*b*), Marshall (1931), Piggott

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(1950), G. C. Taylor (1965), and Wheeler (1968).

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Compounding people and compounding interest

One of the most difficult concepts for many students to understand is how a "trivial" rate of population growth can lead to severe ecological problems for a population. They are dubious when demographers express concern that the annual growth rate of the human population is 2 or 3 percent.

The concept becomes easier to grasp when the notion of how long it takes a population to double its size is presented. The "doubling time" is simple to estimate from the rules of compounding: divide 70 by the growth rate. Thus, a population growing at 2 percent per year will double in 35 years and one growing at 3 percent in 23 years. Bank accounts work in the same manner: the balance will double in 7 years if the interest rate is 10 percent.

We will return to problems associated with population growth in Part III but, in order to continue the argument, some basic notions must be introduced. A single reference should suffice for the present—Ehrlich, Ehrlich, and Holdren (1977).

First, it must be understood that *any* positive rate has the potential for increasing a population to infinity. Eventually there would be standing room only for human beings on this earth whether the growth rate was 0.0001 or 1.0 percent per year. For the first value the doubling time would be 100,000 years and for the second 70 years. We saw earlier ("The Ecological Importance of Tools") how the growth of the human population in the Paleolithic amounted to no more than an increase of 3–15 individuals per year per *million* individuals (0.0003 to 0.0015 percent).

Second, the size of a population is important in relation to the carrying capacity of the environment, that is, the number of individuals that the environment can support (see Hassan 1981, ch. 10 for a discussion of carrying capacity). This will depend, of course, on the species. The number of bacteria that can be supported in a single human intestine is greater than the number of elephants that could be supported by the entire earth.

"Carrying capacity" is not a constant. There are good years and lean years. The resources available in the good years will put a limit on the maximum size the population can attain. When the lean years come, as they always will, the resources available are not sufficient for this population of maximum size. Starvation and/or migration of individuals are the usual solutions.

Thus we will observe another variant of Liebig's Law of the Minimum. Your students may wish to explore this matter by speculating on the course of events in two model populations. In one population the individuals require 5 years to reach sexual maturity; in another population the time required is 6 months. Both live in an environment with a cycle of 3 good years and 1 bad year. What might one hypothesize the fluctuations in population size to be? E. P. Odum (1971, pp. 188–195) can be consulted to check the hypotheses.

Third, apart from migration, the only way a population can escape the constraint of the years with few resources is to increase the resource base. This happens to some extent in many animals—food sources normally ignored become acceptable.

The human population has been unique among organisms in artificially increasing its resource base. When our ancestors were living essentially as hunter-gatherers, as they did throughout the Paleolithic, a very large amount of real estate was required to supply the needed resources. The invention of agriculture greatly expanded the resources that could be obtained per hectare. The invention of irrigation meant that land that otherwise could not supply resources could now do so. The consequences of all these developments were most dramatic. If we can accept the estimates, more people were living in the Sumerian city of Ur than on the entire earth at the start of the Paleolithic.

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Throughout history human populations have attempted to avoid environmental restrictions on population size by increasing the resource base and by migration to those portions of the world with fewer people or inhabited by people who could be conquered. There are, in addition, examples of societies that have attempted to control the size of their populations (Douglas, 1966; Langer, 1972; Wrigley, 1969).

Fourth, in species where the parents care for the young the resources provided by the parents will be divided among the young. The parents may or may not be able to provide enough for all. The European swift is an insectivorous bird that normally lays two or three eggs. In a good year, when insects can be caught readily, most nestlings survive. In cold, wet years, when insects are scarce, there is not enough food for all the young and the usual result is that the strongest nestling is the only survivor (Lack and Lack, 1951). Even in the good years when all nestlings survive, those from the larger clutches are often in poor shape.

In another study Lack (1948) compared the weights of nestling starlings from broods of 2 and 7. He found that at 15 days the average weight of nestlings in broods of 2 was 88 grams and in broods of 7 it was 71 grams.

Fifth, although the potential for any species with a positive rate of increase is to reach infinity, a variety of negative forces invariably prevents this from happening.

A generation ago Foerster, Mora, and Amiot (1960) showed that if the human population continued to increase at the rate it has since A.D. 1, it would reach infinity in the year A.D. 2027. That means that the surface of the earth would be entirely covered, oceans and all, and we would be a mass expanding into space at the speed of light.

There is little doubt that the calculations are correct but we can be sure that the prediction will not come to pass. The truly important question for humanity, however, is "*What will prevent the fulfillment of the predictions?*"

Foerster, Mora, and Amiot also extrapolated the growth curves backwards and estimated that the total human population 1 million years ago was 200,000, which is in good agreement with the estimate from anthropological studies given earlier in this Essay. (A good round number to remember as a reference point is their estimate for the year A.D. 1, which is 100 million.)

Six millennia of population change

We saw before ("History begins at Sumer") how Woolley was able to use archaeological data to estimate the population of Ur. Similar attempts have been made for Egypt (Butzer, 1976; Mitchell, 1982; and Gallagher, 1981). One can estimate the amount of land cultivated, the probable size of the harvest, the food needed per individual, and then put all these numbers together and obtain an estimate of the total population. One can also study skeletons and determine the age at death, sex, and possibly even a rough estimate of the number of children born to a woman (by studying the female pelvis). There was an abundance of such material in Egypt but, unfortunately, the early archaeologists were not interested as we are today in such information and they destroyed countless cemeteries.

The estimates are given in Table 5. The total land cultivated was about 16,000 square kilometers in 4000 B.C. This remained nearly constant so long as the cultivated area consisted solely of the land covered by the annual Nile flood. About 1600 B.C. the shaduf came into use (Fig. 6). This was a primitive, though efficient, mechanism for raising water. It consisted of a bucket tied by a rope to a long pole. The pole was balanced on a fulcrum to decrease the effort required to lower the bucket into a well and then raise it and empty the water into irrigation ditches. (Sometimes this was done by having a person walk along the pole from one side of the fulcrum to the other.) This made it possible to cultivate more land and to water small kitchen gardens and fruit trees throughout the year.

In 1902 a dam was placed across the Nile at Aswan. This was nearly two kilometers wide and about 50 meters high. It backed up the Nile for about 270 kilometers and

TABLE 5. *Egyptian demography: 4000 B.C.–A.D. 1980.*

	Total population	Cultivated land (sq. km)	Individuals (per sq. km)
4000 B.C.	323,000	16,100	20
3000	816,000	15,100	54
2500	1,589,000	17,100	93
1800	1,931,000	18,450	105
1250	2,862,000	22,400	128
150	4,872,000	27,300	178
1000 A.D.	1,600,000	—	—
1800	3,854,000	—	—
1846	4,476,000	—	—
1907	11,287,000	—	—
1927	14,178,000	—	—
1937	15,921,000	—	—
1947	18,967,000	—	—
1960	25,984,000	—	—
1970	33,071,000	—	—
1975	37,011,000	—	—
1980	42,200,000	38,000	1,115
Percent increase from 4000 B.C. to 1980 A.D.	13,100	236	5,600

Data from Butzer (1976), Mitchell (1982), and Gallagher (1981).

provided enough water for irrigation throughout the year. In 1970 the Aswan High Dam was completed. It is more than twice as high, twice as long, and holds back eight times as much water as the earlier dam.

In the past, the total Egyptian population had its ups and downs. More recently it has had only ups. Butzer (Table 5) estimated the total at a third of a million in 4000 B.C. This grew slowly during the golden centuries of Egyptian history and reached a peak of about 5 million in the two hundred year period from 100 B.C. to A.D. 100. By late Roman times the nation was wracked by invasions and foreign domination and the population decreased greatly in size "as a result of managerial incompetence, religious strife and civil war, epidemics, and the devastations of Arabian beduin" (Butzer, 1976, p. 92). Society was disintegrating.

Estimates of population size became more accurate in the 19th century when the population size had returned to its earlier peak (Table 5). The rate of increase in the 20th century became alarming—about a four-fold increase from 1907 to 1980. One obtains a more vivid picture of what is happening when the population data of Table 5 are plotted (Fig. 7).

The number of individuals per square kilometer of cultivatable land started at 20 and rose rapidly to a peak of 178 in Roman times. Data for the early centuries of the Christian Era are not shown but one can make reasonable guesses. Today the number is 1,115 per km². Your students might find it interesting to compute the available space per individual in 4000 B.C. and in 1980.

Thus in a period of 6,000 years the area cultivated has increased 2.36 times, population size 131 times, and density 56 times. The population *added* between 1975 and 1980 is more than the total population at the ancient peak near 150 B.C. See also Hassan (1981).

The dam solution

By the close of the 19th century it was obvious that something had to be done about the pressing problem of overpopulation. The population was increasing rapidly and the levels of poverty and hunger were unacceptable. At that time Egypt was a colonial possession of Great Britain and the British, as noted before, attempted to ease the problem of hunger by building the first dam at Aswan. The argument was that more water would be available to increase the land cultivated and to allow crops to be grown throughout the year. One of the important crops had become cotton, which could be exported to pay for the importation of items that were unavailable in Egypt.

Sir William Willcocks was the designer and builder of the dam at Aswan that was completed in 1902. He described (1901) why the dam was needed:

> Egypt today is in a state of transition. That basin irrigation, which has been typical of the country for 7000 years, is giving place everywhere to perennial irrigation, and the current is so strong that individual views are being abandoned, and from one end of the country to the other there is an eager demand

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FIG. 6. The shaduf in action. The bucket at the lower right is filled with water, raised by the long pole with the counter-weight, and emptied into the irrigation ditch (to the left of the man in front, center). Many of the individuals working in the water will acquire *Schistosoma*. The aquatic larvae of this blood parasite enters a human being by boring through the skin. Nile Valley about 1910. Keystone-Mast Collection of the California Museum of Photography.

that double crops per annum shall replace the ancient single-crop system. The science of manuring and rotating crops on one hand and the practice of draining and irrigating by rotation on the other, have made such rapid and simultaneous strides, that lands can now be made to produce their two and even three crops every year and still retain their full vigour. The rich soil of the Nile valley, with its wonderful climate and still more wonderful river, may safely be trusted to

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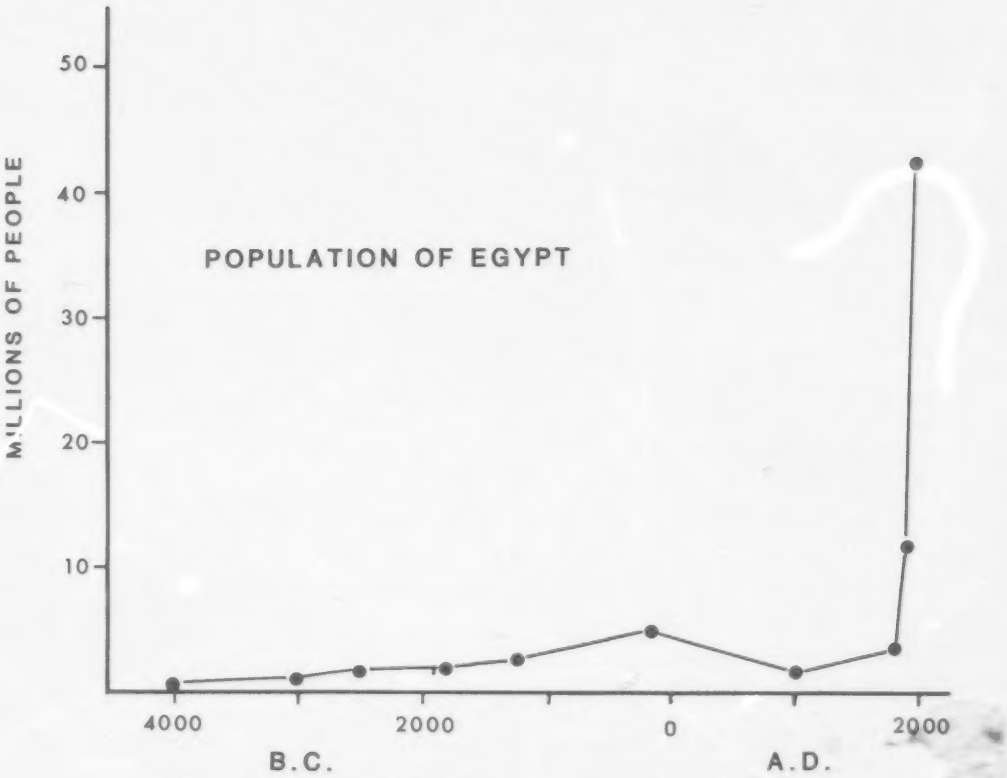

FIG. 7. Six millennia of population change in Egypt. Data from Table 5.

produce the full measure of whatever may be possible elsewhere.

Egypt possesses 6,250,000 acres of cultivable land. Of this area, only 1,730,000 acres are irrigated to-day by the ancient or basin system of irrigation, while 4,520,000 acres nominally receive perennial irrigation. The existing summer supply of the Nile in low years, which is the real gauge of perennial irrigation, suffices for only part of this large area. The remainder is waiting for that increase which can be supplied by reservoirs alone . . . . It has been calculated that Egypt needs for its perfect development 30,000 cubic feet per second of summer supply. Even in poor years the Nile may be counted on for 8000 cubic feet per second, leaving 22,000 cubic feet per second to be provided by reservoirs. Years of low supply should always be taken in the making of such calculations, for mean years are of no value since the surplus of one year is not available for the next. Each year must stand on its own base, and there will never be any stable development of a tract of country depending on irrigation unless all possibilities of periodical years of drought and deficiency are put beyond the power of occurrence.

The benefits were predicted to be enormous. The ability to have a summer planting would mean that 600,000 acres of sugar cane and cotton could be grown, with a value of 20 million pounds. Nevertheless, the dam as approved would be able to sup-

ply only about a third of the water needed. The rest might be obtained by a series of other dams that would impound the needed water. One solution would be to place a dam near the headwaters of the Blue Nile to capture the water during the rainy season and then allow it to flow downstream throughout the year. This would allow perennial irrigation. But, notes Sir William, "it might not be convenient on political grounds to put one of the great public works of Egypt at the absolute mercy of the Abyssinian Emperor" (p. 9).

Willcocks was an engineer and although the construction of a dam at Aswan would be exceptionally difficult he knew that

> there are hard men in the world who would undertake and execute all the works which I have very roughly sketched out in spite of the inhospitable regions in which they are placed. (p. 26)

And it would be worth it all for the Aswan dam would "usher in an era of prosperity in Egypt which will surpass the wildest estimates which the most sanguine have dared to form." Sixty years later Ivan Komzin (1963), the chief Soviet engineer for the construction of the Aswan High Dam, was nearly as optimistic for what his dam would do for Egypt.

When the Aswan High Dam was under construction in the 1960s, one of the main purposes was to increase the area under irrigation and so provide the food necessary for the rapidly increasing population (Table 5). But neither the hoped-for fruits of the Aswan Dam of 1902 nor the Aswan High Dam of 1971 have been fully realized. Sir William's projected era of prosperity never arrived: the per capita income in Egypt was only $8.62 per week in 1977. Nor did the Aswan High Dam solve the food problem. More people were added to the population during the time the dam was under construction than could be fed with the food produced with the additional water the dam was to provide.

The man-made world

Before human beings started to "improve" it, the Valley of the Nile was one of the richest natural regions on earth. The warm climate allows crops to be grown year round. When the un-dammed river was allowed to flow across the farm lands, the fertility of the soil was never destroyed.

Clearly damming the Nile at Aswan was a mixed blessing. We can use it as an example of some of the consequences of human beings altering the environment in the hope of increasing the resources available to them. And, in the jargon of the day, doing so without first preparing a proper environmental impact study.

The thrust of the remainder of this essay will deal with the serious impact of the rapidly growing human population on the natural world. After we finish this review of life in the Nile Valley for the past six thousand years, the longest record we have of unbroken civilization, we will pick up the story again circa A.D. 1 and review how the human population, especially in Europe, became ever more skilled in obtaining the requisites for life. This process started slowly in the Mediterranean world during Classical times, was nearly static in the Middle Ages, took on new momentum in the Renaissance and Age of Discovery, and became a process of enormous power from the time of the Industrial Revolution to the present.

There is no more important topic for students to attempt to deal with in a serious, sustained, and informed manner than these questions of the impact, which is often disastrous, of human beings on the environment. It is important that they be actively involved and that the usual lecture approach give way to a forum involving all. This is especially important since there are no hard answers. Different individuals will reach different conclusions depending on their knowledge, background, politics, ethics, and hopes for the future of the human enterprise. Students often become restive and ill at ease when they are not told "the answers" but there are few answers for the most important and most pressing human problems. A course in biology should provide information, a balanced consideration of the tradeoffs, and a disciplined approach.

So back to the Aswan High Dam of the Nile. What were the benefits and the con-

sequences of this truly great triumph of technology? Different students will reach different opinions but teachers who employ the approach being recommended will observe that the original diversity of student opinion is, with time, replaced by much more uniformity. This in itself is a most hopeful sign because it suggests that a similar accommodation might be possible in society at large—given the chance. And something that is equally hopeful is that students almost always reach a consensus that is both humane and ecologically sound.

The problems in Egypt are not unique. They are rapidly becoming problems of the entire world. To be sure they are exacerbated in the poorer and less developed nations, but no nation, developed or not, can count on a sustaining environment in the future.

One of the most surprising things of all is that every serious environmental problem that confronts the human population has at least a theoretical solution. The difficulty is, however, that in so many instances these possible solutions are totally unacceptable for political, religious, or humane reasons.

Consider this example. Let us suppose that the entire Nile Valley, from the earliest days to the present, was devoted to cattle raising and that the human population consisted only of those directly concerned with caring for the animals. Furthermore, let us assume that the entire valley is controlled by one or a few individuals whose aim is profit on a sustained basis. We can be sure that the owners would be most careful to regulate the size of the herds so that the carrying capacity of the land is not exceeded. Intelligent husbandry would require that the herds be kept at levels that would allow the growth of sufficient vegetation ample for their needs. Each year the herd would be cropped—to keep the numbers from exceeding the carrying capacity of the valley and to provide profits for the owners. An equilibrium condition would exist since the essential elements that departed with the cattle in meat and hides would be replaced by the Ethiopian sediments washed down by the Blue Nile. Barring a drastic climatic or geological change, this system of producing resources for a limited number of human beings could continue indefinitely. It would not be much of a problem to decide what is best.

Although human beings can make decisions of this sort for animals, they are essentially unable to do so when their own welfare is at issue. The carrying capacity of the Nile Valley for human beings is great and a moderate size population could be supported, again for the forseeable future. Depending on the available technology one might guess that a well fed, well clothed, well housed, secure, prosperous, and highly civilized population of from 5 to 10 million human beings could live in the Nile Valley.

There is no possibility, however, of the Nile Valley supporting indefinitely a huge population that is rapidly increasing in size. Once the carrying capacity has been exceeded, the result will be destructive modifications of some aspect of the environment. These may result in pronounced short-term benefits for the human population but there is always the possibility, some would say inevitability, that the long-term consequences would be catastrophic.

But how could one reduce the current population of more than 40 million (Table 5) and reverse the curve of Figure 2? It seems impossible but remember that, today, the Chinese are dealing with a similar problem and their solution is to enforce the rule of one child per couple (Keyfitz, 1984).

That is indeed a draconian solution. Would your students agree to it? Few people enjoy thinking about solutions that are at odds with their notions of human freedom and of ethics, especially if they are not immediately life threatening. Roger Starr (1970) may be correct when he writes:

> I am afraid that if the world is in fact ending . . . men and women will sooner let it end than make the changes in their ways necessary to save it.

But let's assume that he is wrong.

In thinking about ecological problems and possible solutions it is helpful to keep questions of this kind in mind:

1. Is the solution for the good of the individual or for the good of society?
2. If the solution is for a present gain, what are the consequences in the long run?

3. Are renewable or non-renewable resources involved?
4. Are the resources being cropped on a sustainable yield basis or are they being exhausted?

One should think of these questions when the costs and benefits of the Aswan dams are evaluated. It is far too early for any reliable evaluation but it is possible, as of 1980, to give an "as of now" report (Walton, 1981*a*, 1981*b*; and for an earlier evaluation, Schalie, 1974).

The benefits of the Aswan High Dam are tremendous. There is now a reliable supply of water for perennial irrigation. One million hectares of additional farmland can be irrigated year round. New desert land—380,000 hectares—is being irrigated for the first time. Hydroelectric power from the Aswan High Dam supplies half of Egypt's needs for electricity.

But there are costs. First, the yearly fertilization of the soil by the Nile flood has ended and artificial fertilizers must be added to maintain the fertility of the soil. This was recognized as a problem when the Aswan High Dam was planned but that was before OPEC existed and when petroleum, from which fertilizer is made, was very inexpensive. The increased cost of petroleum is offset in part by the new power from the dam, which runs the fertilizer factories.

Second, the Nile formerly deposited silt along the banks of the channels in the incredibly rich delta. Now these banks are being severely eroded and are not replaced by the yearly deposition of silt. This will become an especially serious problem if the barriers between the freshwater lakes of the delta and the Mediterranean are eroded away. That would allow the salt water from the Mediterranean to move into the water table of the delta and greatly reduce productivity. And what is happening to all that silt? It is being deposited in Lake Nasser, the reservoir formed by the dam. This deposition will begin to be a problem in about 500 years and in 1,400 years the lake will be completely filled.

Third, the ancient problem of salinization has appeared:

> The Aswan Dam, which harnessed the Nile in the sixties, will allow further extensions of the irrigated area, but has eliminated the historic natural soil desalination process of the Nile Valley. Waterlogging and salinity, on both old and new farmlands, are becoming major headaches for the Egyptian government, and coping with them demands tremendous expenditures and technical skill. (Eckholm, 1976, p. 118)

Fourth, the Nile sediments that originally flowed into the Mediterranean supported a large population of sardines, which were an important source of protein for the Egyptian population. They are gone. However, there is now a new and even larger fishing industry based on Lake Nasser.

Fifth, there are additional human problems. Thousands of Nubians, who lived along the river banks that are now at the bottom of Lake Nasser, had to be relocated and had to drastically change their life style (Fahim, 1983).

Sixth, the water table downstream from the dam is rising and undermining the foundations of ancient temples, such as Karnak, and thus endangering important artistic and historical resources. This is far from a trivial matter considering that tourism is an important source of foreign currency for Egypt.

Seventh, there was the fear that parasitic diseases would increase. For millennia parasites have been a serious problem for human beings living in the Nile Valley. Malaria, hookworms, and blood flukes have had severe debilitating effects on the inhabitants, especially in the rural areas. It was predicted that increasing perennial irrigation would lead to a great increase in the snails that are the vectors of *Schistosoma* (blood flukes). The data are not too reliable but it now appears that this did not happen. There may have been an early increase but now the incidence appears to be decreasing. More will be said about parasitic diseases shortly.

How does one balance the books? Walton's (1981*b*, p. 36) verdict is this:

> The Aswan High Dam is perhaps best characterized by a drastic solution to a drastic problem. With a population

threatening to grow much faster than supplies of water and arable land, Egypt faced the necessity of doing something.

But has the problem been solved at all? Has the Aswan High Dam assured a long-term prosperous and humane future for the people of Egypt? In fact, is there *any* solution for a human community demanding more resources than the available environment can supply?

And, with reluctance, one should add an eighth possible threat imposed by the Aswan High Dam. In the far from peaceful Middle East, war is a probability, not merely a possibility. The destruction of the Aswan High Dam with nuclear bombs would mean the destruction of Egypt in the ensuing flood.

In addition to the references already given, Lytle (1977) has provided an extensive bibliography on the Aswan High Dam.

The Three Horsemen and population control

The symbolism of only three of the Four Horsemen of the Apocalypse (Revelation 6:1–8) is certain. The Rider of the Red Horse "was given power to take peace from the earth and make men slaughter one another; and he was given a great sword." The Rider of the Black Horse represents famine (or, more accurately that a worker's wages were not sufficient to purchase enough food for survival). The Rider of the Sickly, Pale Horse was Death "with the right to kill by the sword and by famine, by pestilence and wild beasts." The symbolism of the rider on the white horse is uncertain.

These three symbolic horsemen represent even today the principal mechanisms that slow the growth of the human population to a degree that prevents, or postpones, a Malthusian catastrophe. The Three Horsemen have been our companions throughout history and their ecological importance is immense. It is astonishing that all are still potent forces controlling our destiny.

The Rider of the Red Horse

In theory, war and all levels of aggression should be simple to prevent yet even today they are facts of life in dozens of the nations of the world and a threat for many more. How can this be? Are human beings innately aggressive? There is an endless debate on this question (Ardrey, 1966; Lorenz, 1966; Alexander and Tinkle, 1968; Lewontin, Rose, and Kamin, 1984). Leaving aside whether or not aggression is innate, answers must be: "some people are aggressive, some are not," "some are sometimes, but not always," and "some are under some circumstances but not under others."

The effective answer is that it is irrelevant whether or not human beings are aggressive. They behave as though they are to such a degree that access to resources is greatly reduced. War has been with us throughout the historical record; it is a fact of human life. The ancient Sumerians squandered and destroyed many of their resources by frequent wars. It is sometimes suggested that wars have not been important in influencing population size because growth curves show only tiny dips for even the most violent wars. It is more accurate to say that the growth curves of the human population already reflect the almost continuous occurrence of wars.

The ecological significance of war is not only that individuals are killed but that resources are diverted from more productive activities. Those in military service must live on the surplus productivity of others; if injured, they require resources and the efforts of others; vast quantities of food and manufactured goods are used for non-productive activities; there may be great destruction of resources required for human life; and there may be considerable destruction of portions of the natural environment. Working for a better world ceases during times of war. War and the threat of war share with overpopulation and disease the distinction of being the most negative ecological forces that affect the quality of life for human beings.

None of this is news nor has it been for millennia. Yet wars continue and the reasons for them have been varied. Over most of human history one reason was the attempt of the "have nots" to obtain the resources of the "haves." The wilder tribes surrounding the valley of the Tigris and

the Euphrates repeatedly attacked, plundered, and destroyed the first cities of civilization.

From the 15th through the 19th centuries, European powers fought, conquered, and claimed hegemony over most of the world. National pride and the desire to save heathen souls were the overt reasons. Less overt reasons were the desire for more resources, especially at bargain rates. The colonial system was originally based on the mother country obtaining raw materials from the conquered colonies, converting these to manufactured goods, and then selling them to the colonies for a good profit.

There are also recurring wars that seem to be based on the desire of a ruler or ruling group for power, or to neutralize the power of a potential enemy. Still another reason for war is a difference in religion or political philosophy. Examples abound today.

At some periods of history and for some people, war has been a culturally endorsed activity. Keegan (1976, p. 316) wrote that,

> To return, moreover, to a much earlier moment in military time, than that of Agincourt, is to encounter a world in which killing, or if not killing then certainly fighting, was the *only* gentlemanly activity.

The chivalrous knights of the Middle Ages regarded feats of arms as their highest calling and their heroic accomplishments were recorded by bards and rewarded by maidens.

In his classic study of the Cheyennes, George Bird Grinnell (1915) has this to say:

> After the question of providing subsistence for himself and his family, the main thing that occupied the mind of the Cheyenne was the protection of his people from the attacks of enemies and the effort to reduce the power of those enemies by attacks on them.
>
> The fighting spirit was encouraged. In no way could a young man gain so much credit as by exhibition of courage. Boys and youths were trained to feel that the most important thing in life was to be brave; that death was not a thing to be avoided; that, in fact, it was better for a man to be killed while in his full vigor rather than to wait until his prime was past, his powers were failing, and he could no longer achieve those feats which to all seemed so desirable. (p. 12)

Grinnell's story of the Cheyenne brave, Mouse's Road, is a vivid example of what this cultural attitude could make men do (pp. 13–17).

And then there were the men of Sparta at Thermopylae and, in this year of the XXIII Olympiad, we should remember the Athenians at Marathon. Death in the defense of one's nation or religion is regarded as a great virtue, although General George Patton is reputed to have said that it is even more virtuous to get the other poor bastard to die for his.

References, some with a special biological emphasis, are Ardrey (1966, 1976), Blainey (1973), Bohannan (1967), Clausewitz (1833), Ehrlich, Ehrlich, and Holdren (1977, pp. 908–920), Holloway *et al.* (1967), Keegan (1976), Leighton (1981), Lorenz (1966), McNeill (1983), Machiavelli (1521, 1532), Mahan (1890), Morris (1967), Stoessinger (1982), Tinbergen (1968), Tuchman (1984), and Q. Wright (1965).

The Rider of the Black Horse

Individuals are subject to starvation; communities are subject to famine. Famine, then, is epidemic hunger. As with war, famine has been a severe ecological problem throughout recorded history. As we noted earlier, Harlan (1975, ch. 1) suggested that prior to the development of agriculture hunger was not a serious problem. Wild nature is assumed to have produced enough food for the very small populations of human beings. The belief that hunter-gatherers generally had satisfying diets is based in part on studies of present day hunter-gatherers. Those in the warmer regions do not seem to suffer from want of food but those in the Arctic and Subarctic may do so periodically.

It is also argued that, whereas hunter-gatherers counted on a large number of

different species for food, early farmers relied on very few. Thus, the failure of the farmer's main crop would spell disaster, whereas his Paleolithic ancestor could merely have switched diets. Aykroyd (1975, p. 4) concludes "Since man became dependent on cultivated crops for most of his food, famine has caused severe suffering and high mortality in many parts of the world." In contrast, M. N. Cohen (1977) believes that famine was a potent stimulus for human beings to develop agriculture in the hope of insuring an adequate food supply.

Irrespective of when hunger and famine first became serious problems, they have been potent forces throughout recorded history. Although the data for the ancient world are far from complete, there are numerous references to famine. The Old Testament is full of them. Abraham left his home (about 1800 B.C.), where there was famine, and went to Egypt (Genesis 12: 10). Later there was famine in the time of Isaac (Genesis 26:1). Joseph and Jacob were forced to move to Egypt because "there is no pasture in Canaan for our sheep, because the famine there is so severe" (Genesis 47: 1–4; see also Aykroyd, 1975, ch. 3). While in Egypt Joseph became a high official and instituted programs to mitigate the effects of famines.

Coming to more recent times, Dando (1980) estimates that in the 17th century at least 2 million people died of starvation, 10 million in the 18th century, and 25 million in the 19th century. Our century will probably be recorded as the time when more human beings died of starvation than ever before in history (Fig. 8).

Data for individual countries are equally dismal. From 100 B.C. to A.D. 1910, China had 1,800 famines, nearly one a year (D. and P. Brothwell, 1969, p. 176). China's sorrow has not ended. Western experts estimated that as many as 27–30 million Chinese died of starvation between 1959 and 1962 during the "Great Leap Forward." In September 1984 Chinese officials admitted that more than 10 million had died and they could not deny the larger estimates.

In recent centuries, catastrophic famines have occurred about one per decade in Ethiopia, once every 25 years in India (with deaths ranging from 1.25 to 5 million each). The Irish Potato Famine of 1845–1848 resulted in the death of one in every eight persons and an equal number who left their homeland and migrated to the United States.

In the thousand year period between 971 and 1971, Russia recorded 100 famines. This was an average of one per decade but in the 19th century the average was one every three years. There were five major famines in Russia from 1891 through 1932, with deaths upward of 5 million in each (Cahill, 1982; Dano, 1980). In spite of political differences between the two nations, Russia purchases huge quantities of grain from the United States each year.

Famine is of significance not only for those who die but in equal measure for those who live. Starvation is not an all-or-none phenomenon. For every individual who dies of hunger there will be many more who undergo severe physiological and psychological damage. For some the damage will be permanent.

Aykroyd (1975, ch. 2), himself having witnessed the terrible famine of 1943 in Bengal (now the Calcutta area of India plus Bangladesh), has described the effects of insufficient food. There is, of course, a wasting of the body. A loss of 10 percent in body weight can usually be tolerated but with a 20 percent loss the individual becomes exceedingly weak, mentally depressed, and apathetic. Death comes when the loss is between 33 and 40 percent. The brain loses weight slowly and, up to the time of death, the starving person can speak, answer questions, and hear. The thought of food becomes an obsession. Sexual desire vanishes. There is a notable indifference to the feelings of others. Reports of cannibalism, sometimes of one's children, illustrate the degree to which human ethical standards can change when a person is dying of starvation. Extreme edema is typical and diarrhea is often a terminal symptom.

In famine the old people and the children suffer the most. Children cannot grow properly without sufficient protein and,

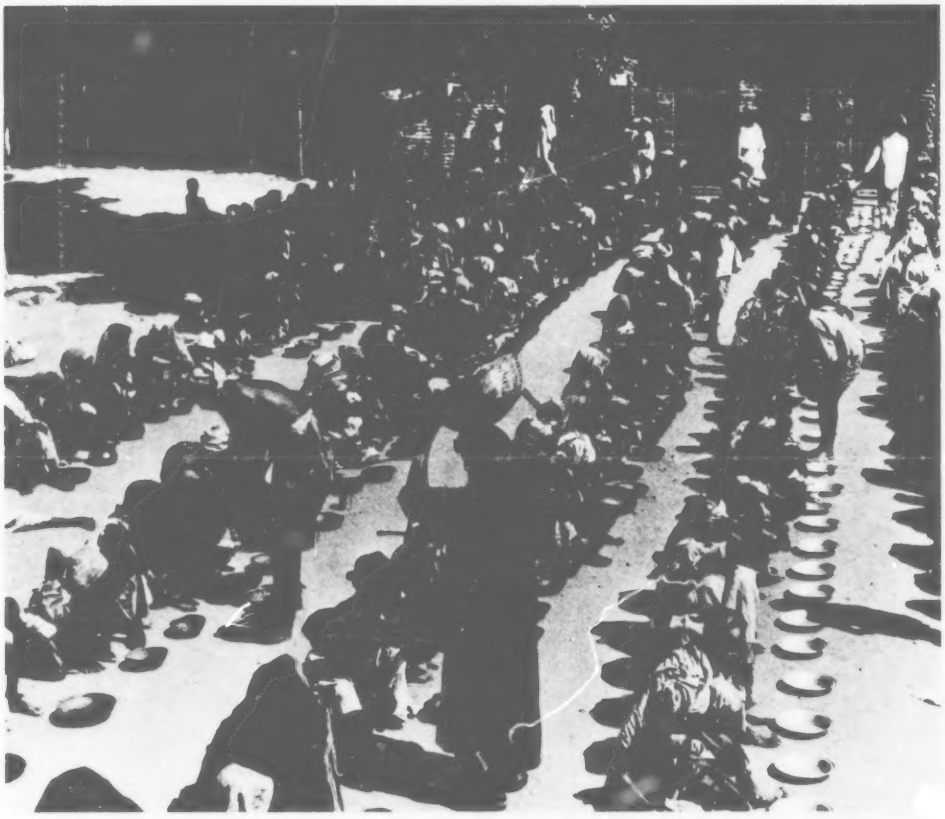

FIG. 8. Famine sufferers awaiting food. Ahmadabad, India. Keystone-Mast Collection of the California Museum of Photography.

when this is lacking, the result is kwashiorkor, a deficiency disease most prevalent between the ages of nine months and two and a half years. The word is of African origin and means "what happens to the first child after the second child is born." The first child would have obtained the necessary protein from mother's milk, a source that ends with the arrival of the next sib. Thereafter the first child would have a diet consisting largely of carbohydrate.

The physiological consequences of starvation are severe but the body has some ways of coping—up to a point. The body's store of protein and carbohydrate is protected and fat is used as the main energy source. Normally the brain cells obtain their energy from glucose but in starvation an interesting change occurs. The cells of the central nervous system begin to produce the enzymes that allow them to use two keto acids, beta-hydroxybutyrate and acetoacetate, both derived from fatty acids. This preserves much of the available protein and carbohydrate. According to Cahill (1970), "This simple adaptation by the brain literally permits weeks of starvation to be extended to months." (This could have been a most important adaptation for the human species upon innumerable occasions.) Since relatively little protein is broken down, the excretion of nitrogen is min-

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imized and is mostly in the form of ammonia.

In severe famine the entire societal structure may crumble. Weitz (1972) argues that the collapse of the Roman Empire was a consequence of famine plus disease. Pitirim Sorokin's (1975) great study on hunger, written when he was starving during the great famine in Russia of 1919–1921, points out the relation of famine and war and notes that starving people will attempt to move to places where there is food and "the main result of hunger, or the threat of it, is war" (p. 223). This was truer in the past than now and is another example of the tension between the "haves" and the "have nots." Sorokin concludes "as long as the size of the population of the world as a whole, or that of parts of the world, is not adjusted to the food supply, war will not disappear" (p. 224).

It is interesting to note that the Black Horse in Revelation (6:5–6) is not identified directly with famine but with the fact that a day's wage was not sufficient to buy an adequate amount of food. Could this have been a reflection of the problems of the city dwellers, no longer able to produce their own food, in late Neolithic times?

Some references to famine are: *Aykroyd (1975), Cahill (1970, 1982), Dando (1980), Ehrlich, Ehrlich, and Holdren (1977, ch. 7 and pp. 627–628), György and Kline (1970), Keys *et al.* (1950), Prentice (1939), Sen (1981), Sorokin (1975), Vicker (1975), and V. R. Young and Scrimshaw (1971).

The Rider of the Pale, Sickly Horse

This horseman is the ultimate for population control—being death in all its aspects—death by the sword and from wild animals, in famine, and from pestilence. Although death from violence may appear to be the major check on population size, Cipolla (1978, p. 89) maintains that the frequent and dramatic declines of local populations are due usually to epidemics and famines. In the past it was not unusual for a local population to be reduced 20 to 30 percent during a famine and epidemic, which often occurred at the same time. In fact, war with its destruction of the resource base for a population was frequently followed by famine and pestilence. McNeill (1976, p. 145) records that the population of China (for which records are the best available for the time) was reduced by war, famine, and disease from 123 million in A.D. 1200 to 65 million by 1393.

Disease has always been a major ecological force for the human population. Again, as with famine, the effects are not only disastrous for those who die but injurious for those who do not. Those diseases well established in a population rarely kill more than a small percentage of those who are infected. This is a consequence of a long co-evolution of host and pathogen, as we have noted before. The host population, over time, usually develops considerable immunity and the pathogen less pathogenicity. It is mutually advantageous for both host and pathogen to survive, which would be the case for neither if the host died. However, the host usually suffers physical disabilities from the presence of the pathogen.

Malaria and schistosomiasis

It is generally believed that malaria has been the most serious human disease throughout history. As late as the 1940s, it was estimated that between 300 and 400 million individuals had malaria (about 10 percent of the total world population) and that about 3 to 4 million of these died each year. The 99 percent that did not die would have been ill for varying lengths of time and have been less able than healthy individuals to care for themselves or for others. They would have been a burden on family and community.

After World War II there was an intensive international effort to eradicate malaria. Much was known about the disease, a potent pesticide—DDT—was available, and there was a "One World" philosophy that found the more developed nations accepting disease as a common problem for all. There were two main approaches: cure the disease by killing the *Plasmodium* with one or another of a battery of effective drugs; destroy the mosquito vector with DDT and destroy its breeding sites.

For a few years it appeared that these public health measures would abolish the

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scourge from the earth but this hope was short lived. Soon the mosquito began developing resistance to the pesticides and the *Plasmodium* resistance to the drugs. Pesticides and drugs were effective agents of natural selection and both mosquito and parasite responded by evolving resistant populations. There were other reasons for the failure of eradication. The dramatic success of the early control measures caused some nations to reduce their control activities. In some instances this relaxed effort may have given the mosquitoes and parasites the time required to evolve resistance. So malaria is still the major human disease and in some parts of the world it is increasing in frequency.

It is probable that the activities of human beings over the ages have increased the prevalence of malaria. The destruction of the natural environment, such as the clearing of forests, often increased the breeding sites of the mosquitoes. Farming, especially of irrigated land, would have meant more water and hence more breeding sites. Poor farming techniques that resulted in extensive erosion would have increased the silt in the rivers. This erosion resulted in marshy lands in the deltas of many European rivers.

Then, too, as the human population grew so did the possibility of *Plasmodium* spreading from one human being to another. The gradual increase in travel throughout ancient times would have brought infected human beings to areas where malaria did not occur. The vector, mosquitoes of the genus *Anopheles*, occurs throughout much of the temperate and tropical regions of the world, including the Near East, Mediterranean basin, and temperate Europe. All that was needed, therefore, was for an infected human being to bring malaria to a community and there would be a good probability that *Anopheles* would spread it.

Human malaria is caused by one of four main species of *Plasmodium*: *vivax*, *malariae*, *falciparum*, and the rare *ovale*. Many other species occur in other vertebrates. The life cycle requires two hosts: human beings and *Anopheles*. The parasite enters the human host via the bite of an infected mosquito and is carried to liver cells, which it enters and reproduces asexually. The newly formed parasites enter the blood stream and penetrate the erythrocytes. Again there is asexual reproduction and each infected erythrocyte bursts, liberating a few dozen parasites. These can invade other erythrocytes, reproduce, and cause the cells to burst. The acute stage of the disease, chills and fever, coincide with the synchronous rupture of huge numbers of erythrocytes. Finally some of the numerous parasites become gametocytes. If these are included in the blood meal of an *Anopheles*, sexual reproduction will occur within the mosquito's stomach. Asexual reproduction follows, producing a huge number of parasites capable of infecting another human being.

For the 99 percent of the victims who do not die, and who represent about 9 percent of all human beings, malaria is a chronic, periodically acute, and severely debilitating disease. The loss in human productivity is enormous. This presents a special problem because malaria is a common disease in many under-developed nations where either being a patient, or having to care for one, is a serious social burden.

There are synergistic relations among malaria and some other conditions. Malnutrition makes individuals less resistant to malaria and to other diseases. The age-old linking of famine and pestilence is valid. There are large areas of the world today where individuals are so malnourished, and at the same time harbor various human parasites and have other diseases, that a high proportion of the population may not know what it is to "feel well."

Malaria remains today a serious problem in much of Central America, northern South America, Africa, southern and southwest Asia, and the islands off southeast Asia—wherever it is warm and moist. It was formerly a problem throughout the eastern and southwestern United States. It still occurs in the United States but the cases are almost always of individuals who have travelled in malarious regions of other countries, contracted the parasite, and returned home. Malaria was a serious problem for our armed forces stationed in Asia and the South Pacific in World War II and in the Vietnam War. There have

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been small epidemics among drug addicts with the vector a contaminated hypodermic needle instead of *Anopheles*.

It is difficult to obtain exact information about the prevalence of diseases in the ancient world caused by organisms that left no trace. There are plenty of accounts of people being sick but it is usually not possible to identify the sickness with a specific disease known to modern medicine. It is a reasonable guess, however, that the human beings in classical times suffered the same diseases as we do today. It is suspected that malaria was serious. Many historians accept that it was one important element in the decline and fall of the Roman Empire and the beginning of the Dark Ages.

There are better records for some of the other helminth parasites of human beings. Many of the mummies from Egypt and elsewhere have been examined for eggs and cysts: and the common parasites in the mummies are the common parasites of today. Some of the genera are *Ascaris*, *Taenia*, *Trichinella*, and *Schistosoma* (Cockburn and Cockburn, 1980).

Schistosoma, the blood flukes, are a serious problem in Egypt today and, as we have seen, there was concern that one of the consequences of the Aswan High Dam would be an increase in schistosomiasis. This has not happened to date but the incidence is already high enough to be worrisome.

There are three important species. *Schistosoma mansoni* occurs in Africa, the Caribbean, and parts of northern South America. *Schistosoma japonica* is found in Japan, China, Southeast Asia, the Philippines, and adjacent areas. *Schistosoma haematobium*, along with *mansoni*, is common in the Nile Valley. The infection rate in the delta region of the Nile averages about 60 percent, with rates as high as 90 percent not being unusual.

Faust, Russell, and Jung (1970) report that there are about 1.3 billion human beings living in areas where schistosomiasis is a problem. Of these about 350 million are likely to be exposed and about 120 million infected.

The life cycle is complex and fascinating and its successful completion requires that ecological conditions be just right. The adults live in the human blood system. In contrast with most trematodes, there are two sexes in *Schistosoma*. The male has a groove (*Schistosoma* means "split body") extending along almost the entire body length. The female is clasped in this groove and may remain so for life. This gentle association is required if the female is to mature (not so for the male). Eggs are deposited in the host blood vessels and from there they bore their way into the intestine or bladder and leave the body in human wastes.

If the urine or feces are deposited in water the eggs hatch, releasing miracidium larvae. Next the miracidium must encounter a snail of a specific species and, if so lucky, bore into the snail's body. There the miracidium changes in form and enlarges to become a sporocyst. The sporocyst reproduces asexually giving daughter sporocysts, which are liberated by the bursting of the original sporocyst. The daughter sporocysts produce another larval form, the cercariae. Cercariae leave the sporocyst, and eventually the snail, to become free in a pond or waterway. To complete the cycle, the cercaria larvae must enter human beings, by penetrating the arms and legs of those who may be working or bathing in the irrigation ditches (Fig. 6). The habit of some natives of washing themselves with contaminated water after defecation provides another opportunity for the cercariae to penetrate the human host.

The chance of the parasite getting from one human being to another may seem slim but the reproductive powers of *Schistosoma* are prodigious. A mature female produces more than 1,000 eggs per day and she may live for months. A single miracidium may be the parent of 200,000 cercariae. It is not surprising, therefore, that the infection rate is so high in areas where so much work demands close contact with water.

In theory schistosomiasis should be simple to eradicate: destroy the intermediate host (the snails) or do not allow human wastes to contaminate water. This is yet to happen and in the meantime this parasitic disease is second in frequency only to malaria and is a severe problem not only

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for the human host but also for the host's nation.

The pathological effects are extensive and caused mainly by the human host's reaction to the eggs. The eggs irritate the tissues as they pass into the intestine or bladder. The spleen and liver become greatly enlarged and the latter eventually becomes cirrhotic. In heavy infections the limbs show extreme wasting and the abdomen may be greatly distended. Abdominal pain is severe, as is the pain accompanying urination in *haematobium* infections where the eggs leave in the urine. The disease is debilitating and, if the load of parasites is heavy, the individual is incapable of working.

Malaria and schistosomiasis are but two of the sorts of interspecific ecological relationships we have with other organisms. They happen to produce the most serious consequences of any parasitic diseases.

These are some useful references to the ecological aspects of human parasitic diseases: J. Baker and D. Brothwell (1979), D. Brothwell and Sandison (1967), Cheng (1973), Faust, Russell, and Jung (1970), de Kruif (1926), Logan and Hunt (1978), *McNeill (1976), Markell and Voge (1981), Noble and Noble (1982), Scarborough (1969), and Zinsser (1935).

In the past, even as now, war, famine, disease, and death took their awesome tolls but on the average the number of babies born each year slightly exceeded the deaths. (Babies themselves contributed greatly to the death rate as did the very old.) Thus the human population continued to grow and for nearly a thousand years, with a mid point at A.D. 1, the Mediterranean World achieved a population large and diverse enough to reach a high level of civilization. First it was centered in Greece and then in Rome. But civilization always results in human populations with more knowledge, power, and technology and this permits their exploitation of weaker human beings and the environment.

Classical civilizations

The Classical World possessed all the basic techniques that were to enable human beings to transform the biosphere more and more for their short term benefits, irrespective of long term consequences. Metals had replaced stone for most tools and weapons. Technical advances were such that great buildings and monuments could be constructed. Techniques for food production had been greatly improved. Donkeys, oxen, and horses were available for transportation and as power machines.

The Greeks were outstanding as artists, philosophers, scientists, and writers. The Romans were their appreciative students and, on their own, carried engineering, military science, and public administration to new heights.

Much of the ability of the Greeks, and especially the Romans, to exploit the environment and weaker peoples was due to the high level of the political and social organization of their societies. This organization was especially effective in the Roman Empire, which in the first century A.D. controlled the Mediterranean basin, the Near East, and Western Europe—the entire civilized world except for China and the New World. Warfare within the empire was restricted to contests for who was to be Caesar; at the boundaries of the empire the Roman legions stood guard against incursions of barbarians.

Trade and travel had reached new peaks. A network of military roads connected all parts of the empire. Larger ships were being constructed and used widely for commerce. The science of navigation was in its infancy. The mariner's compass was yet to be invented. When the coast line was not visible, the captain could only guess the ship's position or rely on the direction of the wind. Latitude could be estimated by the angle of the North Star above the horizon but, in the absence of an accurate clock, it was not possible to determine longitude (that is why Odysseus had such a hard time finding his way home). When Rome was powerful it was even possible to travel safely—a luxury not always enjoyed even to this day.

Physicians and surgeons were beginning to believe that diseases could be the consequences of natural phenomena and not the machinations of an angry god. That insight suggested that preventive and cura-

tive medicine were possible. Nevertheless the cause of disease was almost always unknown. The ministrations of the physicians involved what has probably been the most potent of all curative agents until recent times—the placebo effect. Public health measures were good. Rome and many cities of the empire had aqueducts that brought pure water to the populace, often from great distances. Public baths helped to maintain a high level of personal cleanliness. Good sanitation was helped by sewage systems that carried human wastes to nearby rivers for disposal.

In classical times the Mediterranean world suffered great ecological destruction. We must accept that environmental destruction has inevitably accompanied civilization. The productivity of a forest may support a few hunter-gatherers but if any appreciable number of human beings are to be fed, the trees must be felled and the land farmed.

The critical factor for the survival of civilization, however, is this: *the natural environment must be converted into a man-made environment that is sustainable.* That is, the man-made environment must be managed in such a way that it continues to be a renewable resource capable of supporting a population that cannot exceed a certain size. The size of the population that can be supported without a constant degradation of the environment will depend on the technical proficiency of the inhabitants. This principle has probably been understood for ages, yet it has rarely been followed. It has been more traditional for those over-using their environment to migrate to other regions or to seize the resources of others instead of preserving their own.

Civilization as we know it is almost entirely a product of the Mediterranean world. The major nations of that region—Egypt, Greece, Italy, Turkey, and Spain—have at various times in the past waxed and waned. Each accomplished great things but then slipped into mediocrity. Interestingly, not a single nation waxed more than once. A variety of reasons are cited for these declines, such as war and disease. One fact stands out: in every case, the carrying capacity of the land was exceeded and the environment was degraded.

The Mediterranean climate is characterized by mild winters and hot summers. Most of the rain, which may be torrential, falls during the winter months. During the hot dry summers most vegetation turns brown. Much of the region is hilly, even mountainous.

The first farmers settled largely in the lowlands along the coasts and river valleys. These would have been the more fertile lands or those more readily cultivated. Where there were forests they were burned or cut to make way for the crops. After a few seasons the soil lost much of its fertility and the people moved on. Eventually there was no further place to go and the farmers had to stay in one place and use the land as best they could. The Mediterranean soil was far less fertile that that of Egypt or even Sumeria but, if the fields were left fallow for one year out of three, some of the fertility was regained.

Greece—the hills wash down to the sea

The problem of too many people for too little land arose in Greece before it did in Rome. The Greeks had two main solutions. The first was to stay home and begin to extend the cultivated fields into the hills and mountains. The second was to send large numbers of individuals to colonize the uninhabited or sparsely inhabited lands around the Mediterranean and Black Sea.

Farming the hills in a region with a Mediterranean climate had predictable consequences in the past, as it does in the present. The natural vegetation that prevents erosion is replaced by crops that cover the ground only during the spring, summer, and fall months. The winter rains fall upon an exposed earth and the topsoil is carried away. If we add the probability of goats feeding on the stubble, erosion will be all the greater.

Long before Greece entered its Golden Age (5th century B.C.), it had lost the ability to feed itself. The Greeks had to resort to a vigorous trade in which they exchanged their manufactured goods, wine, and olive oil (the vine and olive tree can grow in poor

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soil) for grain. Thus, the Greeks lived on the primary productivity of other regions.

In the fourth century B.C. the philosopher Plato gave this description of what had transpired (modified from *Critias*):

> Long ago the soil far surpassed all others and its yield was most copious. Such was the natural state of the country. It was cultivated by true husbandmen, who made husbandry their only business. They had a soil that was the best in the world, water was abundant, and the climate was eminently temperate. The district could maintain a great army exempt from all tasks of husbandry. But in the succeeding years torrential rains carried the soil from the higher levels off to the depths of the sea. What remains is like a body wasted by disease for, with the rich friable soil washed away, a mere skeleton of the land is left.
>
> Before this happened, the high hills were covered with soil and trees. But now some of the mountains can afford sustenance only for bees. In earlier times the mountains provided unlimited fodder for cattle. But the trees were felled for huge buildings—some of the rafters are still in place for us to see.
>
> Before the land became barren, the soil benefited from the yearly rains. A plentiful supply of water was received and stored in the soil, that from the higher regions percolated into the lowlands. There were many springs and streams. Now the water runs off the barren ground and into the sea. Today we see abandoned shrines at places where springs formerly existed—attesting to the truth of what is said.

Even Plato's concern was not new. Two centuries earlier some leaders suggested that grain be planted only in the lowlands. The hills, they argued, should be reserved for olive trees and grape vines, which would help to prevent erosion. But more and more people demanded more and more food and the hills were farmed as long as a crop could be obtained. Then the exhausted farms were left for sheep and goats, which further destroyed the vegetation.

It took only a few centuries for the topsoil of the Greek hillsides to wash into the sea. Even the lowlands were damaged. The rapid runoff after rains caused the rivers to flood. Silt blocked the channels in the flat lands and marshes were produced. This land became unsuitable for agriculture but provided excellent breeding grounds for *Anopheles*—and an increase in malaria resulted.

The decline and fall of the Roman soil

The high civilization of Greece lasted only a few centuries, that of Rome nearly a thousand years. Both civilizations were based on the productivity of the soil so one might conclude that the Romans preserved their natural resources more carefully. Not at all—they were better organized and were able by force of arms to conquer the entire Mediterranean world and adjacent regions and exact resources from them.

Until 500 B.C., when the Roman Republic was already established, the land had not been abused. At that time Rome controlled about 1,500 square kilometers, one third more than the area of New York City. The population is thought to have been between 60,000 and 130,000. Taking 100,000 as a reasonable guess, that would mean about 1.5 hectares per person.

Nearly all of the farms of Rome were on a relatively flat coastal plain. The main crops were wheat, barley, and millet, and some vegetables. Very little meat was eaten. The early Romans were primary consumers (or herbivores). They seem to have eaten well, though frugally.

The fertile soil and temperate climate were able to support this fairly dense population and the republican Romans developed a remarkable social, political, and military system. They prospered and procreated but in occasional times of food shortage conditions became unbearable. The response was conquest, first of their neighbors and eventually of the rest of the known world.

But neighbors have to eat also, though not as well as the conquerers. Intensive agriculture in the adjacent Italian countryside led to the loss of the soil's fertility.

Cereals no longer produced good crops and much of the land was planted with the olive, fruit trees, and grape vines. Some of the land was used for grazing because meat had become an important article in the diet of the more affluent Romans. Large tracts of land were abandoned. Erosion of the hills silted the waterways and formed marshes. (By 200 B.C. a huge area between Rome and the sea had become the Pontine Marshes. The marshes became a home for mosquitoes and with them there was an increase in malaria. It was not until our century that the Pontine Marshes were drained and the land turned back to farms.)

After 200 B.C. the Romans were unable to feed themselves from the farms of Italy. Their food, mainly grain, was imported largely from North Africa, Sicily, Syria, Spain, and Egypt. The solution to the problem of more people requiring more food continued to be conquest until about A.D. 100. Then the Romans stopped conquering, not because they had become more benevolent but because their legions were no longer able to extend the bounds of empire.

With no further additions of arable land and no additional victims from whom to extract tribute, the Romans suffered increasingly severe grain shortages. The Emperor Domitian (A.D. 51–96) recognized the growing problem and forbade the planting of more vineyards in Italy and the provinces were to cut their vineyards in half. The land so freed was to be used for grain. However his proposal was not realistic because most of the land that had been planted with vines had already become too infertile for cereals.

About A.D. 300 the Emperor Diocletian again tried to solve an ecological problem with laws. He decreed that farmers must remain on the land so that more food could be produced. But the problem was not the loss of farmers so much as the loss of the soil's fertility. Many had left the land for the free grain and circuses of Rome in part because the land was too poor to farm (as many as 200,000 indigent persons were kept at public expense). The land seemed to be "dying" but the basic cause, as well as the cure, was to remain conjectural until the 19th century.

The reasons for the Decline and Fall of the Roman Empire were complex but the usual negative ecological forces were central: the destructiveness of war, disease, and famine. These three elements are usually related in human history and possibly the most basic is the imbalance of population size and available resources, especially fertile soil. As the soil of Rome lost its fertility, the soils of other areas were overexploited to feed the Romans.

Eventually all collapsed. Rome, then, had its ecological crisis as did Greece in an earlier century and as had Sumeria in the forgotten past. "The glory that was Greece and the grandeur that was Rome" (Edgar Allen Poe, *To Helen*) passed and the western world sank into the Dark Ages, which were to last a thousand years. Much of the Western World lay fallow.

Although there was some regeneration of the natural environment of the Mediterranean World during the Dark Ages, much of the region to this day appears to be irreversibly damaged. So much of the topsoil has washed away that, even if all further human activity ceased, hundreds of years would be required for its restoration.

The tall cedars of Lebanon (*Cedrus libani*), which once formed extensive forests, are now reduced to groves of a few hundred trees (at least they still existed before the present wars started). In ancient times these magnificent trees, upwards of 25 meters tall with trunks 12 meters in circumference, were the only trees that could be used for large buildings. Solomon used cedar beams for his palace and temple (I Kings 5). The huge logs were sent as far away as Babylon and Egypt for the construction of temples and other large buildings. Had the cedars been cropped at a rate that would not have exceeded their replacement, they would still be a valuable resource for the people of the Near East. But the land has been so badly damaged by erosion and goats after the cutting of the trees that it is improbable that the forests could be reestablished today.

This example of concern for the present needs and ignoring the future needs was paralleled by the way the early settlers treated the forests of the eastern United States, and is being repeated with the redwoods of the Pacific States and the magnificent coniferous forests of southern Alaska. The rapid destruction today of the forests in southern Asia and in tropical America to supply firewood for the burgeoning populations is doing severe ecological damage.

Our stewardship of the land, on which all depends, has rarely been farsighted or benign. For centuries this was not a major concern. If one region or one resource was destroyed, human beings could move on to other regions and other sources for the essentials of life and civilization. Today that option is becoming less and less possible.

After a thousand years Europe emerged from the Dark Ages but the centers of civilization were no longer Greece and Rome. Places that had escaped the earlier environmental destruction saw the rebirth of the arts, literature, sciences, more effective governmental administration, and the general improvement in the lives of ordinary people. One of these places was northern Italy where, by an accident of history, there had not been destructive farming. The immensely fertile soil of the Po Valley contributed to the Renaissance, which was based in Florence, Venice, and other northern Italian cities.

Somewhat later Western Europe (north of the Alps and Pyrenees) joined the new wave of prosperity and progress. Western Europe has fewer problems with its soil than do the Mediterranean countries. The climate is cooler, there is more rain the year round, the native plants grow throughout much of the year, and much of the land is flat. These factors mean that erosion and depletion of soil fertility are not as great as in the Mediterranean countries.

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Grabbing the world

The Renaissance, that revival in Europe of learning and of the human spirit, which began in the 1300s and crested in the 1400s and 1500s in Italy, spread throughout Europe. One of its consequences was a desire to know more about other lands. This led first to exploration and then to expropriation of the entire world—at least those regions that appeared to have sufficient resources to make conquest worthwhile.

The sea, the largely unknown sea, was to be the effective path to empire. Nevertheless the ability to construct seaworthy ships and to navigate beyond the sight of land was limited. A prince of Portugal, Henry the Navigator (1394–1460), assembled a group of scholars to collect all that was known of geography, navigation, and seamanship. This information was to make possible the great voyages of discovery that, in a single generation, discovered (for Europeans, that is) a sea route to the Indies, found the New World, and circumnavigated the earth itself.

Bartholomew Diaz sailed down the west coast of Africa and reached the Cape of Good Hope in 1488. In 1497–1499 Vasco da Gama started on the same route but, after rounding the Cape, sailed north along the east African coast and then across the Indian Ocean to India. He had discovered a sea route to the Indies, probably the most important event in the history of Portugal because that was the start of her empire.

Christopher Columbus, later Admiral of the Ocean Sea, while seeking a route to the

Indies not controlled by the Portuguese, inadvertently ran into the New World. In four expeditions (1492, 1493, 1498, and 1502) he explored what is now called the West Indies and parts of the north coast of South America.

In 1519 Ferdinand Magellan and 270 sailors in five vessels attempted to reach those resource-rich Indies by sailing west. He went down the east coast of South America, through the Straits of Magellan, and then had a terrible trip of two months across the Pacific. Crews could not remain healthy on voyages of such duration. The lack of a balanced diet meant that scurvy was to be expected. Magellan was killed in the Philippines. By this time only two of his vessels remained. They sailed south to the Spice Islands, now the Moluccas, where they loaded spice. One vessel was ultimately wrecked and the last remaining ship, the *Victoria*, finally reached home with a crew of 18 under Juan Sebastian del Cano, the first captain to circumnavigate the world.

In a single generation an enormous wealth of new lands and resources had opened up. Conquest and exploitation followed rapidly. The Portuguese claimed the east for themselves and maintained their position by force of arms. By 1520 they had a fair knowledge of the geography of India and the islands southeast of Asia. They became dominant in trade in spices and other luxury goods from the east, formerly controlled by the Moslems and the Venetians.

The Spanish concentrated on the New World. Columbus and others had established some colonies in the West Indies and these became bases for the conquest of Mexico in 1519 by Hernando Cortes (Prescott, 1843) and of Peru in 1532 by Francisco Pizarro (Prescott, 1847).

The ecological consequences of these voyages of exploration and conquest were immense. The entire world was opened to the ravages of the most technologically advanced people of the time. No native people could withstand them for long. There was intense competition among the European nations, which based their claims for new lands upon discovery.

Of course the lands had already been discovered and occupied by the native people who must have been somewhat puzzled when some bold explorer came ashore, planted his nation's flag, and claimed all the vast land in the name of his sovereign. But once a claim was made, it was necessary to maintain it by force of arms. The rivalry between Spain and Portugal became so intense that the two nations appealed to Pope Alexander VI to divide the New World, in a just manner, between them. Alexander proposed a north-south line 100 leagues west of the Cape Verde Islands and said that Portugal should have all to the east and Spain all to the west.

Eventually nearly the whole world was claimed by the European nations. Though Spain and Portugal claimed all of South America, France, Holland, and Great Britain were able to secure small areas. Central America was nearly all Spanish, as was the southern and western part of what is now the United States. France claimed Canada and, in time, Russia took charge of Alaska and the Pacific Coast down to central California.

Australia, New Zealand, and many nearby islands became British. Southern Asia was divided among the British, French and Dutch. China and Japan remained nominally free but, from time to time, China was occupied by foreign troops sent in to protect the foreign merchants. Africa was divided among Great Britain, France, Germany, Italy, Belgium, Spain, and Portugal. The region that each nation claimed was based mainly on what they had the power to hold. As a consequence, the African nations today are not based on racial affinities but on the historical realities of power politics, which accounts for some of their more serious problems.

Colonial possessions were of value to the mother country not only for the products they supplied but also as new homes for the excess population. Just as Greece and Rome had sent their surplus inhabitants to found colonies, the European nations sent their surplus citizens across the seas. Much of the New World, Australia, New Zealand, and much of eastern and southern Africa were originally inhabited by hunter-

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gatherer people, with their characteristic low population density. Today the New World, Australia, New Zealand and South Africa are peopled mainly by those of European ancestry.

There has been much speculation why the Europeans, of all people, grabbed the world, but the quest for additional resources must have been paramount. The Spanish kings needed gold, or other items of value, to support their military adventures. Portugal grew rich through its control of the spice trade. New France (Canada) was a source of valuable furs and fish for the mother country. European cities required raw materials for their manufactured goods and customers in the colonies to buy them.

There appears to be no instance of a nation using the procedures of sound husbandry in its exploitation of a colony. It was rare enough to do so at home, so it is not surprising that steps to protect the environment in such a way that the colonies would remain a viable source of resources were not taken. European power was becoming an increasing factor in environmental destruction worldwide. This power was to take a quantum increase at the time of the Industrial Revolution, which ushered in our world of today.

The Industrial Revolution

In the middle of the 18th century there began in England a movement that was to alter greatly the relations of human beings with one another and with their environment. It was a movement, therefore, of great ecological importance. The name applied is "Industrial Revolution" but scholars are careful to point out that every important event and phenomenon of the Industrial Revolution had its antecedents. The term "revolution" is appropriate, however, because of the rate of change. In only a few generations human beings developed a far greater ability to exploit their environment, especially for nonrenewable resources, and to produce goods and services in vastly greater quantities. Human beings became far more powerful and far more technologically proficient.

The techniques of the Industrial Revolution spread from England in the late 18th and 19th centuries throughout Europe and to the enclaves of European people overseas (including the United States, which adopted the techniques and attitudes of the Industrial Revolution with enthusiasm). This was but the beginning of a period, quantitatively different from any that had gone before, that continues to this day. Mankind has, in our generation, achieved the quintessence of power—the ability to destroy itself and the biosphere. We combine that power with a system of moral responsibility that is probably little changed since the days of the beginnings of civilization in Sumeria. That is the awesome horror of our times.

The Industrial Revolution involved important political, social, economic, and technological changes. In early 18th century England most goods were produced by individuals or small groups of craftsmen working in their homes or shops. The products were to a considerable degree individual creations for which the craftsman could take pride and responsibility. It was a system that remains on a small scale today: much of the Harris tweed is still produced by individual weavers working their own looms in their own cottages.

The Industrial Revolution replaced the cottage industry with the factory system. The workers who operated the factories came from rural areas, where improvements in agricultural productivity meant that fewer farmers were required to grow the surplus food to support those in the towns. Machines began to do many of the things that formerly were accomplished by human hands working with simple tools. Uniformity of product began to replace individual variations. The worker, once responsible for the entire product, now guided a machine that made only a part.

The Industrial Revolution saw a large increase in the use of coal and iron. The forests of England had been largely consumed and efficient ways were found to burn coal. England was fortunate in having a good supply of coal and iron ore. One of the most important machines of the Industrial Revolution, and of all time, was the steam engine. Prior to its invention, power

FIG. 9. The power of steam. The ax of the loggers in the left photograph, except for being made of steel, is similar to the common cutting tool that human beings have used for at least a million years. It would have been beyond the ability of the two loggers to move the huge trunk once the tree had been felled.

was limited to that of human beings (self, servants, employees, slaves), domesticated animals (ox, horse, mule, donkey), wind (windmills, sailing ships) or water (mills for grinding grain, cutting logs, pumping mines). All of these, we should note, are based on renewable sources of energy. The steam engine, when coal fired, depended on a non-renewable source of energy.

A horse can do about ten times the work of a man, but even the early steam engine, as perfected by James Watt, could do the work of a large herd of horses. An American railroad locomotive of 1835 developed 100 H.P. and by 1860 ones developing 560 H.P were in service (J. H. White, 1968). The steam engine was used first to pump water from deep mines. Later it became the central power source for the factory. In contrast with windmills and water mills that were stationary sources of power, the steam engine could be con-

The Industrial Revolution and its steam engines, such as the locomotive in the right photograph, provided power equal to that of hundreds of human beings. Northern California about 1903–1905. Keystone-Mast Collection of the California Museum of Photography.

nected with the wheels of locomotives (Fig. 9) or the propellers of ships.

There were great improvements in transportation. A railroad network began to grow across England, joining sources of raw materials, factories, cities, towns, and ports. Roads were improved and soon they approached the degree of excellence of those constructed in England by the Romans.

The living conditions of the workers in the early decades of the Industrial Revolution were grim and permitted only a marginal sort of existence for most. Hours were long, housing usually poor, food inadequate, educational opportunities limited, and health care almost nonexistent. But slowly conditions improved.

Karl Marx (1890, ch. 10) gives a vivid description of the inhumane working conditions in 19th century England. He did not have to exaggerate or distort the evi-

dence to make his point—his data were drawn from official governmental reports. Some people were, quite literally, worked to death.

Factories required large inputs of capital for machines and labor and, to show a rich profit, had to produce and sell large volumes of products. This required large markets and was an important reason for Great Britain's Empire—to buy the products of England's factories. It was necessary also for government to adopt a laissez-faire attitude toward industry, an attitude very different from that of earlier systems that held a heavy hand on the activities of the citizens. Industry was allowed to compete, since it was assumed that in the long run the most efficient would prevail. In the middle of the 19th century this philosophy seemed to be validated by Darwin's (1859) *On the Origin of Species.* Thus competition was not only appropriate for the industrial world but it was the rule for the world of life.

The Industrial Revolution organized society into an efficient system for exploiting the natural world and producing an abundance of products and services that continues to this day. Unbridled human power was unleashed upon the environment. Today no product or technological process seems impossible so long as the laws of nature are not disobeyed. Feats once reserved for the gods are within our powers. The consequences of this can be good or bad—depending wholly upon human decisions and human behavior. The final section will attempt an appraisal.

References

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Special topics II

Suggestions for topics that might be the basis of short oral reports by students continue here with those appropriate to Section II.

Jericho. So far as is known this city of Israel has been inhabited almost continuously since the early Neolithic Period. No other site provides such a continuous sequence of archaeological materials. See K. M. Kenyon (1967).

Biblical sledge still in use. Isaiah (41:15) mentions a sledge for threshing grain. The same type, with pieces of flint embedded in the base, is still being used. See J. Bordaz (1965).

Camel saddles. They greatly increased the usefulness of camels for riding and carrying burdens. See R. W. Bulliet (1983).

Religion circa *12,000 B.C.* A Stone Age site in Spain seems to have been a shrine. See L. G. Freeman *et al.* (1983).

Loss of habitat for birds. More people mean more houses and less space for trees. See D. S. Wilcove and R. F. Whitcomb (1983).

A surviving Stone Age culture. On a Pacific island. See J. S. Athens (1983).

How to read Harappan. Much can be learned about ancient life and its ecological problems if there is a written record. The Indus Valley Civilization had a script that is now being deciphered. See W. A. Fairservis (1983).

Indigenous European culture. The standard view that European culture was derived from the Middle East is being revised. See Colin Renfrew (1971).

Rice from U.S. farms. California helps supply the world's need for rice. See J. N. Rutger and D. M. Brandon (1981).

Rice. It feeds more of us than any other single food and has a fascinating biology. See M. S. Swaminathan (1984).

Ancient warships. Some were powered by 4,000 oarsmen. See V. Foley and W. Soedel (1981).

Mining in the ancient world. For lead and silver. See N. H. Gale and Z. Stos-Gale (1981).

Salt in the soil. It has been a problem for 5,000 years. See A. F. Pillsbury (1981).

Stone Age hunter-gatherers in Ireland. They were there 9,000 years ago. See P. C. Woodman (1981).

Why are there no pigs in Scotland? This ecological-anthropological study attempts to provide an answer. See E. B. Ross (1983).

China's approach to population control. The nation with the world's largest population is trying to set a ceiling with compulsory family planning. See N. Keyfitz (1984).

First lessons in writing and mathematics. At the dawn of civilization in Sumeria. See J. Friberg (1984).

An epidemic of measles in Iceland. Its path could be followed from city to city and then to rural areas. See A. Cliff and P. Haggett (1984).

Americans circa *19,000 B.C.* They settled in a cave near Pittsburgh and stayed for the next 20,000 years. See J. M. Adovasio and R. C. Carlisle (1984).

More food from the sea? Yes, if we change our methods of harvesting. See B. J. Rothschild (1981).

Farming the sea. In can be done in seaside ponds. See J. H. Ryther (1981).

Food from Antarctica. The cold sea has an abundance of organisms. If carefully cropped they could be a valuable source of food. See J. R. Beddington and R. M. May (1982).

Measles and rubella. They are nearly eliminated from the United States. See S. Krugman (1983).

Indian fires. They cleared the land that was later used for the farms of European settlers. See S. J. Pyne (1983).

Mold spores and disease. They cause Valley Fever in the arid regions of the Southwest. See D. Pappagianis (1983).

Tool-using by an insect. A bug's method of capturing termites. See E. A. McMahan (1983).

Food preservation in Colonial America. A present-day attempt to live as did our ancestors. See J. Anderson (1982).

A 6,000 year bison hunt. The Indians started stampeding them over a Canadian cliff by 3700 B.C. See B. O. K. Reeves (1983).

Stone henges and social structure. The erection of these stone monuments required considerable political control and planning. See C. Renfrew (1983).

III. 1984—HUMAN ECOLOGY IN NORTH AMERICA

Prelude to the present

We tend to overlook the fact that the first people to discover America were those who crossed the Bering land bridge from northeast Siberia to Alaska many thousands of years ago. The first Europeans appear to have been the Vikings, who made visits at least as early as A.D. 1000 but did not settle.

The Spanish started the conquest and colonization of the New World with the voyages of Columbus. They expanded to Middle America with the expedition of Cortes in 1519. Moving north they settled at St. Augustine in Florida in 1565 and, far to the west, they settled Santa Fe about 1609 and San Francisco in 1776.

The first French settlement in Canada was in 1604, nearly a century after Jacques Cartier had claimed the land for France. Searching for furs, the French moved along the waterways of the St. Lawrence, the Great Lakes, and the Mississippi to reach the interior. They settled the lower end of the Mississippi Valley in 1699. The Russians extended their claims down the Pacific Coast from Alaska and in 1812 reached Fort Ross in California. The Dutch, following the discoveries of Henry Hudson, settled Manhattan Island in 1624.

After the abortive attempt of Sir Walter Raleigh to found a colony on Roanoke Island, off North Carolina, in 1585, the English settled at Jamestown, Virginia in 1607. The Pilgrim mothers and fathers reached Plymouth, Massachusetts in 1620, the Calverts settled in Maryland in 1634 and William Penn in Pennsylvania in 1682.

Eastern America was inhabited by Native Americans who varied greatly in cultural attainments. Some were hunter-gatherers and others agriculturalists. (The Maya and Aztecs to the south had developed high civilizations.) Metal, if available at all was used mainly for ornaments, not for tools. There were no wheeled vehicles and no

beast of burden, except for the dog which was sometimes used by western Indians.

The date of the arrival of the first Americans is conjectural, with estimates varying from 12,000 to 100,000 years ago. Gowlett (1984*a*) suggests we use 30,000 to 15,000 years ago until we know better. When the Europeans arrived, once again, might made right and they claimed the land for themselves. Though vastly outnumbered, the Europeans prevailed because of their social organization and far superior technology. The natives were either killed, enslaved, intoxicated, expelled, or subjected to diseases for which they had no immunity. Few American Indians remain today east of the Rocky Mountains.

The settlers coming to the United States were claiming possession of one of the richest natural environments on earth. As Captain John Smith put it (1624, vol. 1, p. 60).

> The mildnes of the ayre, the fertilitie of the soyle, and situation of the rivers are so propitious to the nature and use of man, and mans sustenance, under that latitude or climat. Here will live any beasts, as horses, goats, sheepe, asses, hens, etc. as appeared by them that were carried thether. The water, Isles, and shoales, are full of safe harbours for ships of warre or marchandize, for boats of all sorts, for transportation or fishing, etc. The Bay and rivers have much marchantable fish, and places fit for Salt coats, building of ships, making of Iron, etc.

It was not fashionable at the time to do environmental impact studies so the land and its resources were treated as though they were inexhaustible.

The eastern part of the country is temperate and well watered; the central portion has some of the richest agricultural land in the world; the west is temperate but more arid. Large deposits of essentially all important minerals awaited discovery and the reserves of coal, petroleum, and natural gas proved to be enormous. The eastern portion, the mountains of the west, and the coastal areas of the northwest were forested with fine timber. Rivers and lakes provided pathways to the interior.

An abundance of game served the protein needs of the early settlers until they developed their own herds of domestic animals. The bison of the short-grass prairies are said to have formed the largest known herds of mammals. The adjacent seas were rich in fish and other edible marine life. The nearby Grand Banks, off Newfoundland, were among the greatest fishing areas on earth. (European fishermen had exploited them from an early date, probably discovering America for themselves well ahead of Columbus.)

Jamestown and Plymouth Rock

In short, the Europeans were coming to the finest remaining natural environment on earth. It must not have appeared as such to them as the first few decades were characterized by hunger, disease, attacks by the Indians, and their life had few of the amenities of Western Civilization. The wealth of America was potential and it took generations of effort, skill, and devotion to realize that wealth.

The ecological problems were enormous but were basically the same as those for any species invading a new territory: means of obtaining resources and successful competition with other organisms of the same and different species.

The main resource required was food. The ships bringing the invaders to the New World could have carried little more food than was sufficient for the very long voyage (mainly against the wind). The settlers brought seeds of the crops of their homeland. The Native Americans, however, were raising many of their own food plants and these had already been selected for productivity under the local conditions.

The Algonquian Indians living in Virginia when Captain John Smith arrived obtained about 75 percent of their food from hunting and gathering and 25 percent from agriculture. Their crops were corn, two varieties of bean, gourds, passionflower, and tobacco (Caldwell, 1971; Feest, 1978). Captain John Smith (1624, vol. 1, pp. 58–59) described the Indian's method of planting corn, which he also calls wheat,

> The greatest labour they take, is in planting their corne, for the Country naturally is overgrowne with wood. To prepare the ground they bruise the barke of the trees neare the root, then doe they scortch the roots with fire that they grow no more. The next yeare with a crooked peece of wood they beat up the weeds by the rootes, and in that mould they plant their Corne. Their manner is this. They make a hole in the earth with a stike, and into it they put foure graines of wheate and two of beanes. These holes they make foure foote one from another; Their women and children do continually keepe it with weeding, and when it is growne middle high, they hill it about like a hop-yard . . . . Every stalke of their corne commonly beareth two eares . . . . Every eare ordinarily hath betwixt 200 and 500 graines. They plant also pease . . . which are the same they call in Italy, Fagioli. Their Beanes are the same the Turkes call Garnanses.

Captain John Smith recorded the Indian's habit of planting corn and beans together. This would be fine agricultural practice—the beans supplying some of the nitrogen required by the corn.

The Pilgrims found that the Indians of eastern Massachusetts grew similar crops (Salwen, 1978). Not only did they share their food with the Pilgrims, thereby preventing starvation, but William Bradford (1912, vol. 1, pp. 215–216) tells how Chief Squanto instructed the newcomers in the local arts of husbandry:

> Afterwards they (as many as were able) began to plant ther corne, in which servise Squanto stood them in great stead, showing them both the manner how to set it, and after how to dress and tend it. Also he tould them excepte they gott fish and set with it (in these old grounds) it would come to nothing, and he showed them that in the midle of Aprill they should have store enough come up the brooke, by which they begane to build, and taught them how to take it, and wher to get other provisions necessary for them; all which they found true by triall and experience. Some English seed they sew, as wheat and pease, but it came not to good, eather by the badnes of the seed, or latenes of the season, or both, or some other defecte.

Squanto knew what he was doing when he suggested that a fish would have to be added to the "old grounds" (i.e. that had been planted before), if a crop was to be obtained. The soil of New England, except for the river bottoms, is very poor. This is mainly a consequence of its geological history. A coniferous forest in a cool moist area produces an acid soil and over the centuries, since the retreat of the Pleistocene ice sheet, it had been badly leached of nutrients. The remaining nutrients were sufficient for some species of native plants but were not sufficient for crops that were removed from the fields with the nutrients they contained. Hence the need for that fish in every hill of corn.

Settling down

One of the greatest problems facing the settlers was clearing the land for farming. Eastern America was almost entirely a continuous forest, magnificent for the naturalist, but an obstacle to life for the early settlers. As Captain John Smith noted (vol. 1, p. 52), "yet grasse there is little or non . . . for all the countrey is overgrowne with trees." The solution was to cut the forest, which required tremendous labor, or to adopt the Indian method of slash and burn (still the principal method in much of Mexico, Central America and South America; Packer, 1973).

When trees are burned the nutrients garnered by them are released to the soil. Planted crops use up these nutrients and then the fields must be allowed to lie fallow and become overgrown by native plants. After a decade or so the nutrients liberated by the decomposition of rocks will have been taken up by the native plants. Then the cycle of slash and burn can be repeated unless erosion removes the topsoil before native plants are able to form a protective carpet (see the illustration on page 71 of Packer's article for an example of what can happen).

In New England the forests provided a

plentiful supply of wood, which served not only for construction but also as fuel. At first most of the items manufactured from metals had to be imported from England but soon there were local mines and forges. Clay was available for pottery and sand for glass.

The ecological problems with other organisms were serious. Although the native animals were of little concern, relations with the Indians worsened after a few years. We generally think of Europeans as having great martial superiority because of their guns. In the early 17th century, however, a person standing at a distance would just be downright unlucky to be killed by a bullet. Once discharged, the weapon would have to be reloaded. During the time required for that operation, a person armed with a bow could get off many arrows with a high degree of accuracy. (The first settlers sported a great variety of arms: the matchlock, blunderbuss, snaphance [Miles Standish had one], wheellock, and doglock [Gluckman, 1965]. The matchlock smooth bore musket appears to have been the weapon most generally available.)

The hostility of the Indians, and at times their French allies, kept the settlers pinned down on the eastern seaboard until shortly after the American Revolution. It was then that the New Englanders were able to leave their poor, rocky patches and seek better farming land elsewhere. They found it in the calcium-rich lands of northern New York state. The farms there gave fine crops until the land became depleted of nutrients and the center of more highly productive agriculture moved west again—to Ohio (Rossiter, 1975).

The ability of the settlers to move west was correlated with a number of new factors. The Revolutionary War had given martial training to many of the men. A large number of new and improved weapons had come to the colonies. These were flintlock muskets: the British Brown Bess and the French Charleville. Apart from these imported military weapons, the production of the famous "Kentucky" *rifles* was a well established American industry (based mainly in the Lancaster Valley of Pennsylvania). By the middle of the 18th century the Kentucky Rifle had become a superb weapon. A rifled barrel is far more accurate than one with a smooth bore. The Kentucky rifle was deadly in the hands of a skilled marksman and, together with the ax, became the essential tools of the frontiersman. These two technological products allowed the settlers to conquer and settle the new lands.

American agriculture, until the time of the Civil War, tended to be "backward and inefficient" Rossiter writes (p. 3). In part this was because there was so much land available that it did not seem necessary to be careful. Then, too, the knowledge necessary to maintain the fertility of the soil was simply lacking. The big change came in 1841 with the publication of the first American edition of Liebig's *Organic chemistry in its application to agriculture and physiology*. Before Liebig the general notion was that productivity depended on "humus" in the soil, although it was not clear what humus was or what it did. This was certainly a reasonable hypothesis, since productivity was usually better in soils with decaying matter and, of course, it was realized that the droppings from cattle, horses, birds, and human beings added fertility to the soil. Liebig advanced a different thesis: fertility was more closely correlated with the presence of essential nutrients such as nitrogen, calcium, and phosphorus.

Go west young man (and companion)

By about the middle of the 19th century, what had been a continuous forest from the Atlantic seaboard to about 98° longitude had been reduced to farms and woodlots all under the control of the European settlers and their descendants. In their slow move to the west, their crop plants had been selected for the climate and soil. The settlers had an abundance of water and the forests provided wood for construction and energy.

Then pioneer farmers came to the edge of the forest and looked out upon a sea of grass that extended a thousand kilometers to the base of the Rocky Mountains. This new environment presented ecological problems more difficult than for any lands to the east. The lack of trees, except along

the river bottoms, meant that wood for houses and fencing was not available. More serious was a deficiency of permanent water. There were rivers and streams but many of them were seasonal. Water holes were widely scattered though, of course, they were adequate to support the tremendous herds of bison and other animals. Melville had this problem of the lack of perennial water in mind when, in *Moby Dick* he had Ishmael say:

> Go visit the Prairies in June, when for scores on scores of miles you wade knee-deep among Tiger-lilies—what is the one charm wanting?—Water—there is not a drop of water there!

And finally there were the Plains Indians —a far fiercer breed of men than the few eastern Indians.

The westward movement of settlement came to a grinding halt. In fact, it took a broad leap to the west coast and then began to move into the vast interior from both east and west. But before any attempt at settlement was made, most of the Far West had been visited by the "mountain men" (Stone, 1956) in search for furs, mainly beaver, to be exported principally to England for making hats.

Walter Prescott Webb (1931) has written the classic study of the ecological problems that European Americans had to solve to become capable of exploiting the plain's environment. Much of what he had to say is based on an earlier United States Geological Survey report prepared by W. D. Johnson (1901–1902).

Before the techniques of farming in this different environment had been perfected and the Indians controlled, the grasslands were used for cattle. This was the time of the open range, when the cattle were allowed to roam wherever they could find food and water. Periodically they were rounded up and driven to market.

This procedure is as old as agriculture itself. Land that cannot be used to raise crops, either because it has lost its fertility or lacks sufficient rainfall for cultivated plants, can be used for grazing. Thus, native vegetation, inedible for human beings can be converted to cow and then used for food by human beings.

The transition to farming depended to a considerable degree on the ability to solve the problems of obtaining water on a year-round basis, to obtain materials for construction and fencing the farms, and to be able to transport produce to market and to obtain manufactured goods in return. The problem of water was solved by the perfection of a new type of windmill that was used to pump water from the huge aquifers that lie under most of the plains (Fig. 10). In the absence of abundant timber, houses were constructed of sod. The problem of fencing was solved by the invention of barbed wire.

The problems of transportation were solved in many ways. Horses were the preferred method for individuals. Sturdy wagons could carry produce for long distances and, except for the hand carts of the Mormons, they were the vehicles that carried people and their supplies from the settled states to the plains and on to the west coast. Then the railroads came. Before the Civil War, Jefferson Davis, the Secretary of War, had sent four army exploring expeditions to the west to ascertain the most practical route for a railroad from the Mississippi River to the Pacific Ocean. Three east-west routes were surveyed and, after the cessation of hostilities, work began on the central transcontinental route. In 1869 the tracks coming east from California met those going west from the eastern states at Promontory Point, Utah.

The wars with the Plains Indians lasted for a full generation after the Civil War and this struggle for natural resources and physical control resulted in the complete domination of the land by the Americans of European descent. The army had become a powerful fighting force during the Civil War and some of its more effective officers were sent west to deal with the Indians.

Another quest for resources had a profound influence on the history of the west—the rush for California gold in 1849 and the subsequent spread of mining activities throughout the west.

The young United States adopted the

FIG. 10. The American-designed windmill made farming possible in the Great Plains and other regions where surface water is lacking but ground water can be tapped. Southern California.

Industrial Revolution with zest and the 19th century established the nation as a leader in technological innovation and production (Figs. 11–12). By 1900 Americans had the ability to use the environment at will.

There is high drama in the young

democracy's march to the west. It was largely an undisciplined march by highly independent people concerned with getting the most for themselves at the moment and not worrying about the ecological tomorrow. America was still boundless and bountiful.

This was the last great expression of that remarkable spirit that began with the Renaissance and saw people who were, to varying degrees, strong, hard, noble, talented, technologically proficient, hard working, despicable, dishonest, determined, greedy, and sometimes fanatical in their drive to conquer the earth. They had all the virtues and vices of today yet somehow the mix and the times were different and the people of Europe, feeling themselves far superior to all others, claimed the resources of the world for themselves. Since World War II there has been a retreat from this near complete hegemony and other peoples in other lands are determining their own destinies.

The conquest of America—references

Since the American experience is so recent, it is still easy to see that our history depends largely on our relations with the environment. Our literature is rich in works that describe the interactions of the environment and the first European settlers to encounter it. You may wish to suggest that some of your students become familiar with this literature—it really is high drama.

The suggestions are for three time periods and three categories. The time periods are from first settlements to the American Revolution; the second from the Revolution to the Civil War; the third from the Civil War to the early 20th century. The first category suggests original documents and descriptions. The second consists of histories and general accounts. The third group, which may have the greatest appeal for humanities and social sciences students, suggests human centered works that include personal accounts of what it was like to attempt to survive in the environment of the place and moment. I have usually shown the date of first publication but most of the titles are available in recent printings.

Settlement to the Revolution. Primary sources: Beverley (1722), Bolton (1908), Bradford (1912), Byrd (1928, 1929, 1940), Carver (1778), Cheever (1848), Franklin (1793), Hariot (1588), E. Johnson (1654), Josselyn (1672, 1674), W. Penn (1683, 1685), Purchas (1613), J. Smith (1624), and Wood (1634).

Secondary sources: J. Barth (1967), *Cronon (1984), Crosby (1972), Hine (1973), Hine and Bingham (1963), Parkman (1849, 1879, 1948).

Human centered: Most of the primary sources and C. M. S. Kirkland (1839), Knight (1825), and Nash (1982)

Revolution to the Civil War. Primary sources: J. R. Bartlett (1854), J. and W. Bartram (1957), W. Bartram (1791), Catlin (1841, 1867), Coues (1893, 1895, 1897*a*, 1897*b*, 1898*a*, 1898*b*, 1900), Dana (1840), De Voto (1953), Emory (1848), Foreman (1941), Frémont (1845), Imlay (1792, 1793), Ives (1861), Jefferson (1784–1785), Marcy (1854, 1859), Montaignes (1972), Nuttall (1821), Pacific Railroad (1855–1860), O. Russell (1955), Schiel (1859), Schoolcraft (1821, 1834, 1851–1857), Sitgreaves (1853), Stansbury (1853), Tocqueville (1850), Wilkes (1845).

Secondary sources: Bakeless (1939, 1957), G. P. Barth (1975), R. A. Bartlett (1974), Caughey (1948), De Voto (1943, 1947, 1952), Egan (1977), Foreman (1939), Goetzmann (1959, 1966), Gregg (1844), Hine (1962, 1973, 1980), Hine and Bingham (1963), Hollon (1955), Irving (1835, 1836, 1837), Manly (1949), Parkman (1849, 1879), Paul (1947), Ross (1855), Sandoz (1958, 1964), Stanton (1975), Stegner (1954, 1964), G. R. Stewart (1962), Stone (1956), Tyler (1968), Wade (1959), and E. S. Wallace (1955).

Human centered: Cooper (1823, 1826, 1827, 1840, 1841, 1845), Melville (1851), Moberg (1983–1984), Nash (1982), Paulding (1831, 1832), Richter (1966), K. Roberts (1937), Stowe (1869), and Thoreau (1849, 1854, 1864, 1865).

The Civil War to the 20th century. Primary sources: A. Adams (1903), Hayden (1873–

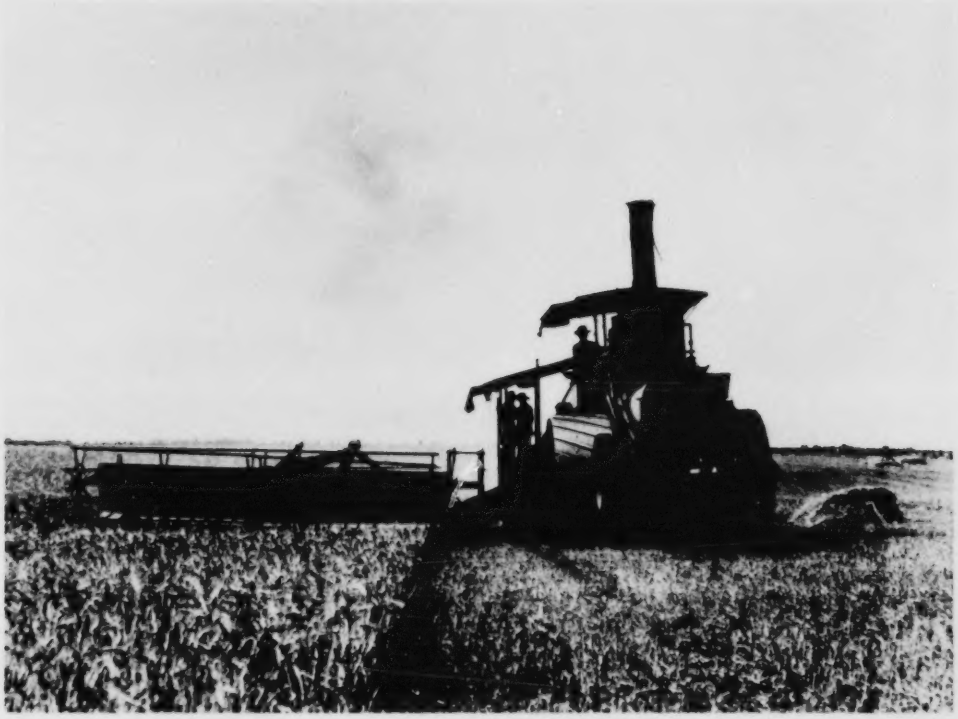

FIG. 12. A steam harvester cutting a 25 foot swath of grain. Tools such as this, and the plows of Figure 11, were responsible for the great increase in productivity of American farmers (Fig. 15). California about 1904. Keystone-Mast Collection of the California Museum of Photography.

capacity of the environment, the environment will be slowly degraded. And, of course, all depends on the nature of the environment—the innate carrying capacity of Antarctica differs from that of the Fertile Crescent. Packer (1973) estimates "that where there are more than 25 persons per square kilometer of cultivated area, degradation of soils and vegetation occurs." That means 4 hectares per person of *cultivated land*. This estimate appears to be based largely on agricultural practices in Africa today.

Now we will scan the tables of the U.S. Bureau of the Census's *Statistical Abstract of the United States 1984* and *Historical Statistics of the United States: Colonial Times to 1970* for information on the trends in population size and technological activity in the United States.

National trends: population and space

The first national census of 1790 found that there were 3,929,214 individuals occupying a land area of 864,746 square miles. That meant an average of 4.5 individuals per square mile, or 58 hectares per person. By 1980 our population had grown to 226,545,805 and our land area to 3,539,289 square miles, which meant 64 Americans per square mile.

Figure 13 shows the curves for population size and number of hectares per individual. Records for Colonial times are poor, but since the population was only 4 million in 1790, the curve must have been nearly

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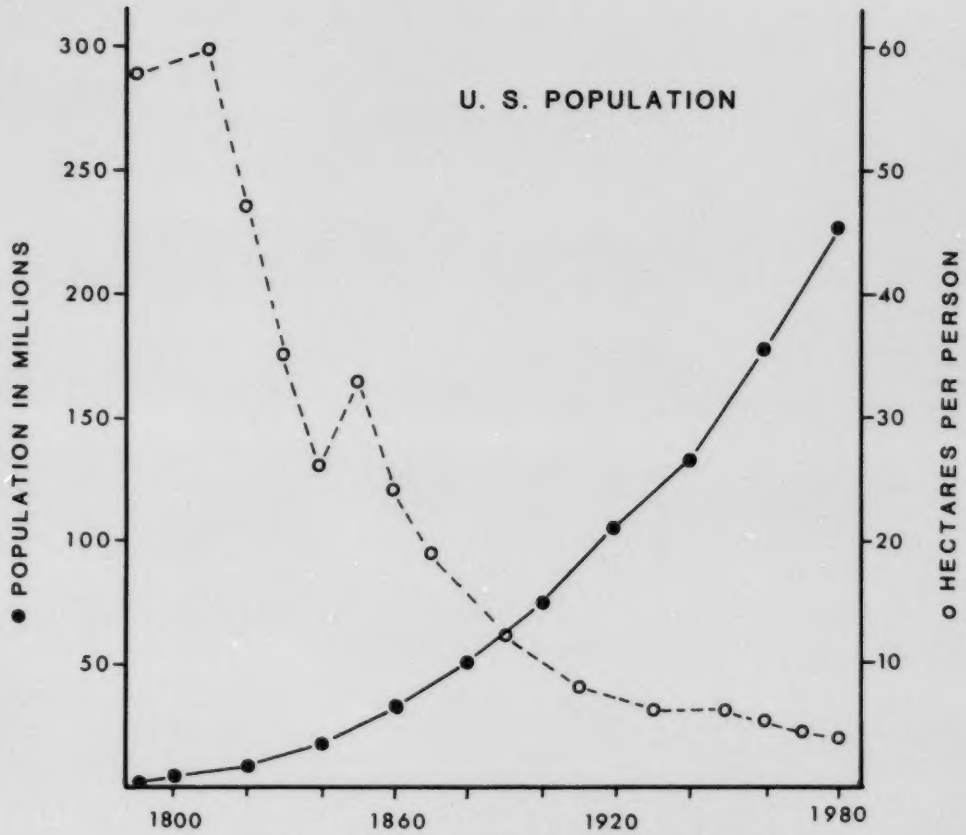

FIG. 13. Population growth in the United States from 1790 to 1980.

flat (on the scale used in the figure) from 1607 until then. One of the more impressive facts is this: it took us 243 years, from 1607 to 1850, to reach a population size of 23 million; in the decade 1970–1980 we *added* 23 million to the population. In 1980 the percentage increase was 1.0, which would give a doubling time of about 70 years. (The value for whites only was 0.9, with a doubling time of about 78 years; and for blacks 1.6, with a doubling time of about 44 years.)

In 1790 there were 58 hectares per patriot and now there are 4. Your students may be initially puzzled by the relatively smooth curve for population size and the ragged curve for hectares per person. Can they offer an explanation? The answer is to be found in the fact that the United States grew in land as well as population: Louisiana Purchase, 1802; Treaty of Guadalupe Hidalgo, 1848; Gadsden Purchase, 1853. The Alaska Purchase of 1867 does not alter the slope since the data exclude Alaska and Hawaii until the census of 1950. Alaska added nearly 20 percent to our land area. If we exclude that huge, sparsely populated area, the hectares per person drops to about 3.6. Remember, these are total hectares, not hectares of cultivated land. Our personal square of earth includes deserts, mountains, arid plains, cities and towns, freeways and parking lots, as well as agricultural land. Cultivated land in the

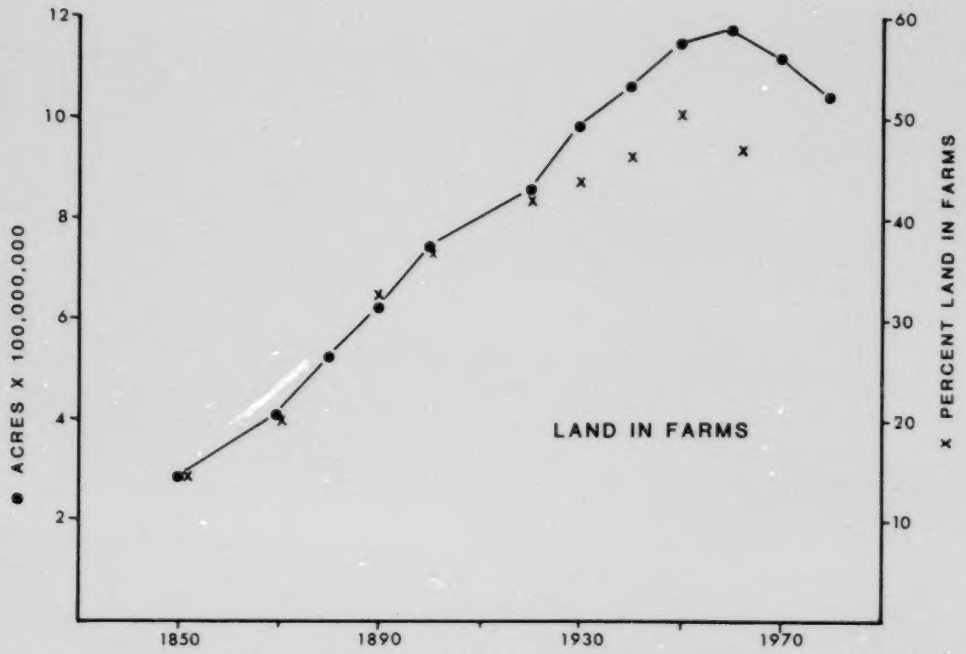

FIG. 14. Total acreage of farms in the United States. The Xs show the percentage of total land that was in farms.

U.S. reached a high of 50 percent in 1950 (Fig. 14). That means that the per capita number of hectares of cultivated land is 1.8.

Agricultural statistics. In 1850 there were nearly 300 million acres devoted to agriculture (Fig. 14). The amount grew until about 1960 and then declined slightly. Not only has the total acreage increased but, until a recent drop, so has the percentage of all land devoted to agriculture.

The United States started as a nation of farmers. In fact, in the 17th century most people in most nations lived and worked on farms. In the developed nations there has been a drastic reduction in recent years of the percentage of individuals on farms. In 1880 the farm population was about 22 million, which represented 44 percent of the total population (Fig. 15). The farm population grew in absolute size until the end of World War I, remained constant for about a decade and then, after 1940, declined precipitously. The percentage is now 2.4.

This decline in the size of the farm population and in the percentage of all individuals engaged in farming is a reflection of the great increases in efficiency. For example, in 1800 it required 56.0 man hours to raise and harvest one acre of wheat. By 1970 it required 2.9 man hours. And there was much more wheat to harvest per acre in 1970. In 1800 the average yield was 15.0 bushels; in 1970 it was 31.0. We can use these numbers to determine the man hours required for 100 bushels: in 1800 it was 373 and in 1970 it was 9. Here are additional examples. It required 344 man hours to raise and harvest 100 bushels of corn in 1800 and only 7 in 1970. It took 601 man hours per bale of cotton (500 pounds) in 1800 and only 26 in 1970.

American agriculture had passed from being the art of husbandry to being a branch of modern technology.

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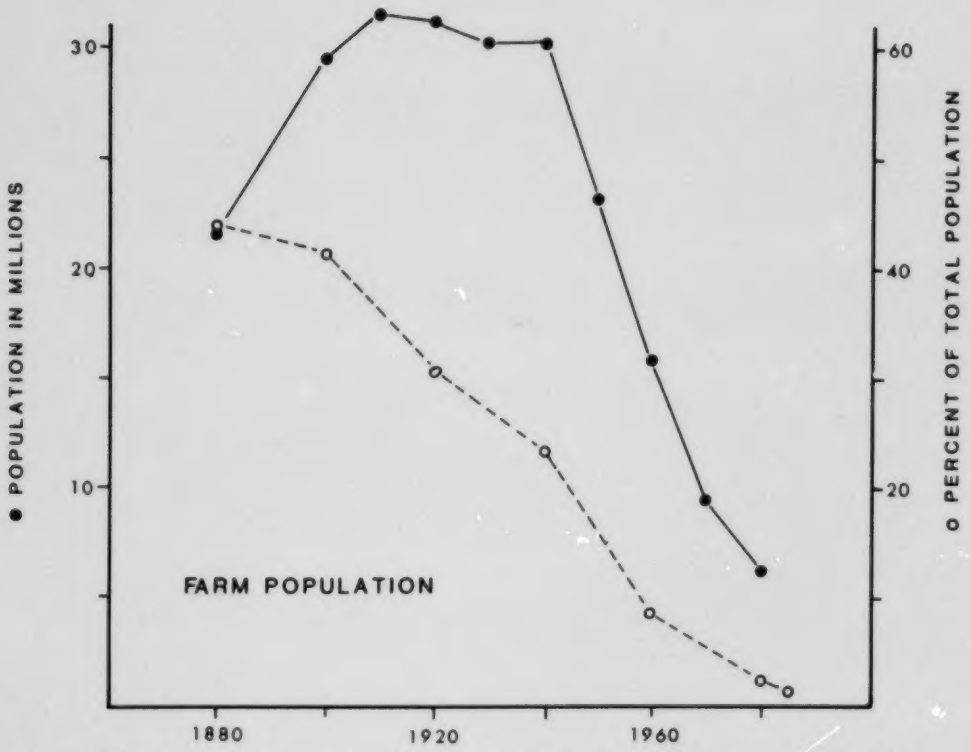

FIG. 15. The farm population of the United States and the percentage of the total population living on farms.

Coal and steel. Data for coal and steel, the basic commodities of technology, give us a good measure of technological activity. In 1800 the total production of bituminous coal was 108,000 tons. The amount increased until 1920, declined during the Depression and again in 1960 (Fig. 16). It is on the rise again.

The data for steel are given in Figure 17. In 1860 the total tonnage produced was 205,000. A high was reached in 1978 with 137,000,000 tons. Since then there has been a slight drop.

Electricity, motor fuel, and horse power. The production of electricity is another good and sensitive indicator of technological activity. The data since 1902 are shown in Figure 18.

In the last few generations the transportation of individuals and goods has come to depend heavily on automobiles, trucks, buses, and airplanes, all of which consume petroleum products. In 1919 annual consumption was 3 billion gallons. This rose to 125 billion in 1978 and dropped to 115 by 1981 (Fig. 19).

One can continue to cite data for different activities, things produced, and things consumed, but the curves are essentially the same—they are rising sharply. One last example will suffice for the moment. It has been estimated that for the United States the total horse power of all prime movers in 1850 was 8.5 million. For 1970 it was 20,408 million—a 2,400-fold increase.

But isn't all this good?

The Delphic Sibyl would have answered "Well, yes and no" and, as usual, been correct.

The products of American agriculture

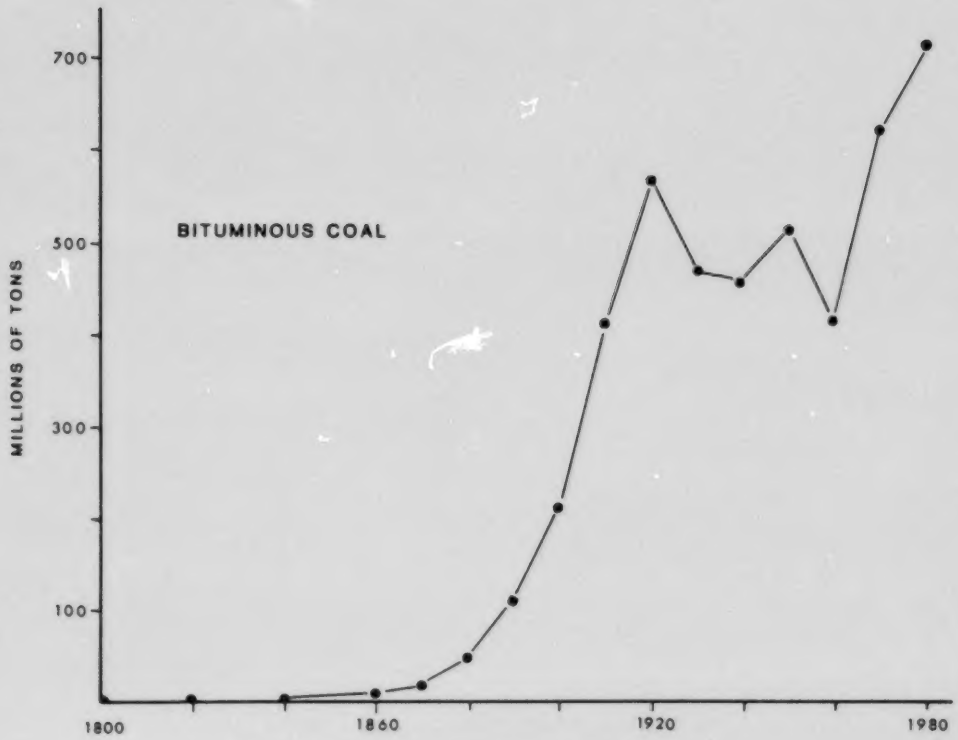

FIG. 16. Bituminous coal production in the United States.

and technology provide our nation with the world's largest amount of food and the world's largest quantity of goods. We have become the greatest consumers of natural resources in a world of want.

Leaving aside the question of whether or not it is right for us to have so much when so many have so little, let's consider some of the restraints on consumption. This is an exceedingly complex problem, and with the large number of published reports and analyses one is likely to be overwhelmed with details. The basic principles are few and simple, however.

1. We live in a finite world and the basic quantities of all consumable products are fixed except for those produced with the sun's energy.

2. The desirable end products of production are often accompanied by by-products that are undesirable.

The first principle deals with two sorts of resources: non-renewable and renewable. The non-renewable resources are those in fixed amounts; that is, there are no natural processes that will add to the existing supply. There is only so much iron, gold, silver, coal, copper, natural gas, zinc, petroleum, lead, and aluminum in the earth's crust. The coal, petroleum, and natural gas that are consumed as fuel or used in manufacturing are gone forever.

The elemental metals could, in theory, last forever. They could be mined, fabricated, and, when the product is no longer desired, recycled. This could be done so carefully that the existing supplies could last almost forever. This does not happen. Although our profligate behavior is being increasingly restrained, we are still a "throw-away society" to an unacceptable degree.

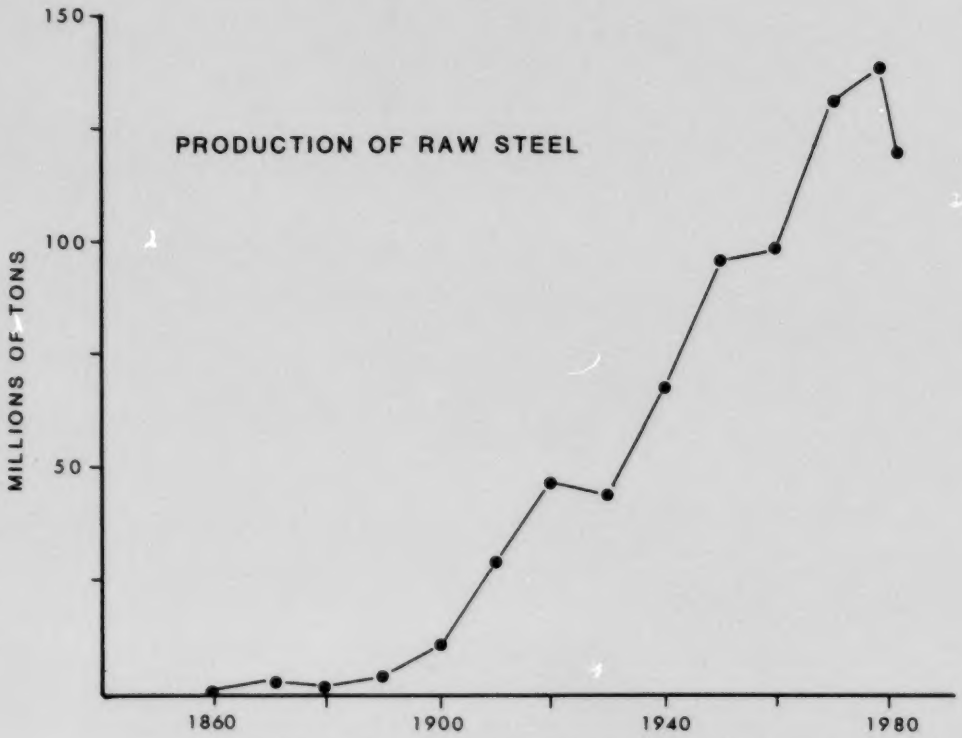

FIG. 17. Production of raw steel in the United States.

Renewable resources are those involved in the solar-powered cycles of the living world as described in Part I of this essay. C, H, O, N, and the other elements move through the autotrophs and heterotrophs in such fine balance that, on a worldwide basis, their concentrations in any compartment of the cycles remain surprisingly constant. Food is produced and consumed and, so long as the organisms remain in the same locality when they die, there is no loss or gain of materials. The water that is evaporated with the sun's energy returns as rain. The evolution of organisms and the concomitant changes in the earth's crust struck a balance that seemed eternal. But that was before serious perturbations were introduced by human beings.

We are finding now that as the numbers of people and the level of their technology increases, the natural cycles are being overloaded. This is a consequence of the second principle mentioned before—the undesirable by-products of desirable technological activity.

One set of problems arises when raw materials are processed to obtain pure samples of some desired substance. The natural world is extraordinarily benign chemically. There are very few places where one will be injured by exposure to chemical substances. This is true even though poisons are widely distributed in the earth's crust: arsenic, sodium, mercury, lead, selenium, chlorine, fluorine, phosphorus, and uranium. While these are violent poisons when pure, they are of little concern in nature because of their low concentrations or because they are combined with other elements to form non-toxic or slightly toxic substances.

Both sodium and chlorine are violent

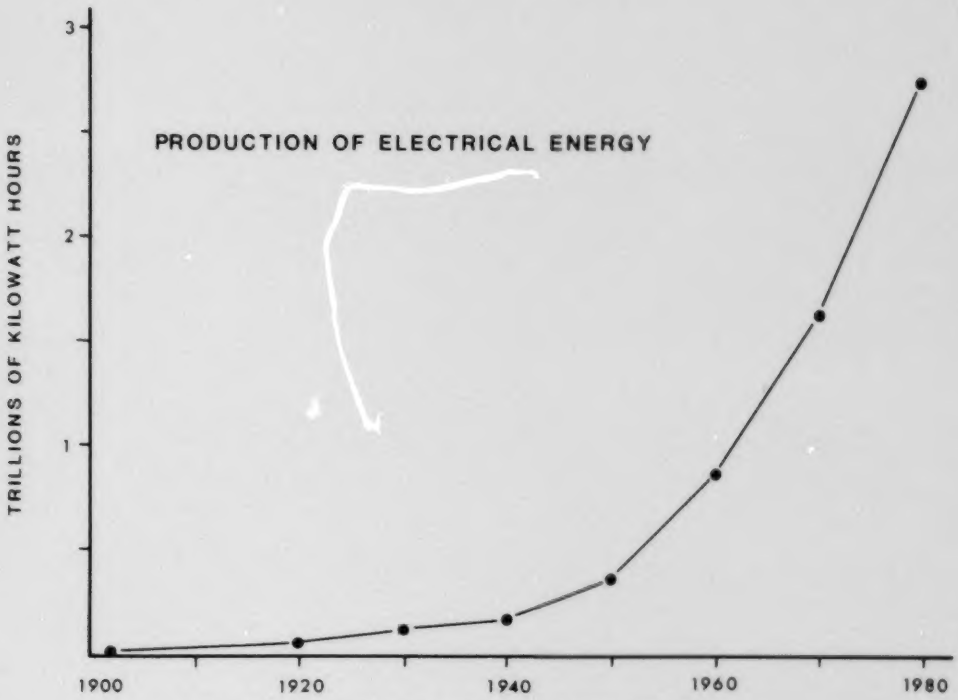

FIG. 18. Production of electrical energy in the United States.

poisons yet their usual occurrence is as sodium chloride in salt deposits or as chloride and sodium ions. Pure fluorine is a violent poison ("rat poison"), yet one locality in Texas has a high concentration of fluoride salts in the drinking water. The most notable result is that the inhabitants have excellent teeth. Uranium and its salts are highly toxic and, of course carcinogenic, yet they are a hazard only to miners and processors of the ores.

And, after all, most of the potentially dangerous chemical substances are in underground ores. Any toxic minerals that might have been on the surface would have broken down long ago and have been diluted with inert materials.

A poison is a substance that has an adverse effect on an organism because of its chemical effect. Not surprisingly, the organisms of today do not find commonly encountered substances to be poisons. They have evolved to live with the existing inorganic world. However, the problem today for so many organisms is that they are being exposed to a huge and expanding list of new substances produced by our factories that they have never encountered before. In time some organisms might be expected to evolve resistance to some of these new poisons. We have the well documented cases of evolution of resistance to pesticides in insects (Georghiou, 1972; Georghiou and Taylor, 1976; A. W. A. Brown, 1971) and to antibiotics in microorganisms (Elliott, 1973). Nevo *et al.* (1984) found an interesting case of microorganisms developing an ability to live with mercury pollution. Thus, should we wish to convert our earth to a cesspool, we shall not be alone.

In addition to these undesirable consequences of obtaining resources, other problems are associated with how we use and dispose of them. If coal and petroleum products consisted only of C, H, and O, burning them for energy would produce

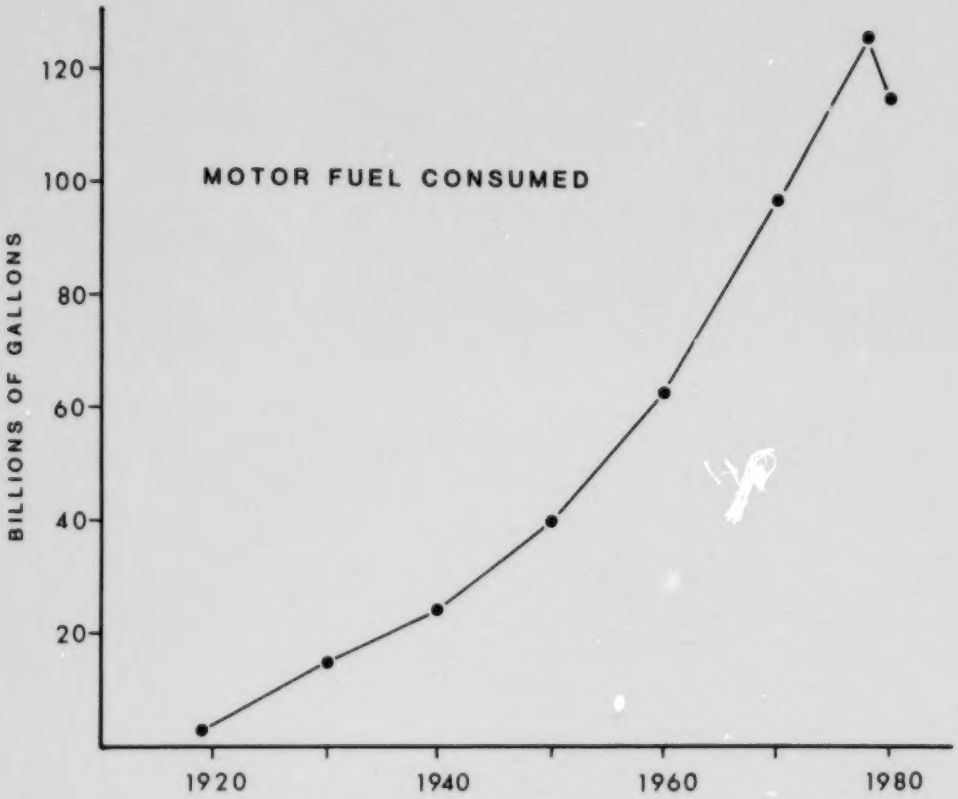

FIG. 19. Consumption of motor fuel in the United States.

only carbon dioxide and water. This would be no more than a normal part of the carbon cycle and the only concern would be what an above-natural increase in carbon dioxide would do to the climate. But these fossil fuels contain other elements and, when burned, they emit a number of undesirable and toxic substances that foul the air.

The 1984 edition of *Statistical Abstract of the United States* informs us (Table 357) that the quantities, in metric tons, of our air pollutants in 1981 were: carbon monoxide, 90,500,000; sulfur dioxide, 22,500,000; volatile organic compounds, 21,300,000; particulates, 8,500,000; oxides of nitrogen, 19,500,000. Thus, the total was 153,000,000 metric tons. That means 674 kilograms for every American.

There are similar impressive figures for wastes produced by industry (Table 360): 132,237,000 metric tons in 1981. The main contributors were the chemical and primary metals industries. Our non-industrial wastes (paper, glass, aluminum, etc. from homes, stores, and offices) for 1980 (Table 361) totalled 104,849,000 metric tons. Of this, only 8 percent was recovered.

Thus the total of these three categories of waste products is 390,000,000 metric tons per year, or 1.72 tons per person. That is about thirty times the total biomass of all Americans—and remember this production of wastes goes on year after year.

Although the above are serious environmental problems that are associated with how we obtain, fabricate, and use resources, there are equally serious problems with

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TABLE 6. *World population: U.S. Bureau of the Census median projections.*

	1980	2000
More developed nations		
Total population	1.17 billion	1.32 billion
Annual percent growth	0.68	0.51
Doubling time	103 years	137 years
Less developed nations		
Total population	3.30 billion	5.03 billion
Annual percent growth	2.18	2.02
Doubling time	32 years	35 years
World		
Total population	4.47 billion	6.35 billion
Annual percent growth	1.78	1.70
Doubling time	39 years	41 years

Source: *Global 2000*, p. 8.

TABLE 7. *Gross national product: Annual per capita, U.S. dollars.*

	1975	2000
United States	7,066	14,212
Western Europe	4,653	9,889
USSR and Eastern Europe	2,591	4,472
Latin America	1,005	1,715
Africa	405	620
Asia (except USSR)	306	557

Source: *Global 2000*, p. 9.

the adequacy of supplies of non-renewable resources and the extent to which we are using renewable resources at a rate greater than they are regenerated. And, of course, the severity of the problems depends on how many people are demanding resources and at what level and in what time period.

First we will consider some general data and then the specific problems associated with air, water, and food.

How long will the resources last?

In 1977 President Carter reminded us that "Environmental problems do not stop at national boundaries. In the past decades, we and other nations have come to recognize the urgency of international efforts to protect the common environment." He created a high-level committee to "make a one-year study of the probable changes in the world's population, natural resources, and environment through the end of the century." The committee's report, *The Global 2000 Report to the President* (1980; the quotes just given are from p. v) is the source of the data now to be given.

Population. Table 6 shows the 1980 data for world population and the Bureau of the Census median projections for what it will be in 2000. The growth rate of the developed nations is now low and is projected to decline. We must remember, nevertheless, that any positive rate that is long sustained will fill up the world eventually. The less developed nations, which now comprise 74 percent of the world's population, are growing rapidly and by the year 2000 are projected to make up 79 percent of the total population. In the two decades before 2000, the less developed nations will *add* considerably more to their populations than the total for the developed nations. These are the nations where poverty, hunger, disease, and some forms of environmental destruction are most severe.

Gross National Product. Table 7 shows the per capita production of the total goods and services available to society—the GNP. Once again there are large differences among the nations of the world and the differences are projected to remain. The GNP for Western Europe is now 15 times that of Asia and is projected to be 18 times by 2000.

Food. Table 8 gives the data for grain—our main food worldwide. The important information is the difference between production and consumption. Of the nations and groups of nations shown in the table, only the United States and Latin America produce more than they consume. That means that most nations import some of their food. Currently the United States exports more food to other nations than do the other exporting nations (mainly Australia, Canada, New Zealand, and South Africa) combined. This will probably be true in 2000 as well. By that time one of the most important ecological problems for the world will be the level of agricultural

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TABLE 8. *Per capita grain production and consumption in kilograms.*

	1985		1990	
	Production	Consumption	Production	Consumption
United States	1,331	924	1,697	1,183
Western Europe	442	503	471	582
Japan	102	376	143	484
Eastern Europe	789	850	922	998
USSR	813	857	903	950
China	238	246	259	268
Latin America	248	244	306	283
Less developed countries	182	203	196	210

Source: *Global 2000*, pp. 93–94.

productivity of the United States and the few other surplus producers of food.

The high value for consumption in the United States is not because of a carbohydrate-rich diet. It reflects the fact that large quantities of grain are fed to our meat-producing animals.

Water. There should be enough water, on a worldwide basis, in the year 2000. The current use is 1,400 trillion meters[2] and in 2000 this is predicted to be 2,800. Severe regional deficiencies are projected, especially in those lands with low rainfall and rapid rates of population growth. The greatest use for water is for irrigation: now it is 70 percent but it is projected to drop to 51 percent by 2000. In the same interval water used in industry and mining will increase from 22 to 41 percent of the total.

Water quality is now a serious problem and projected to become more severe. Water continues to be the main sink for waste disposal and as the wastes increase in quantity and toxicity, water quality will decrease.

Energy. Table 9 gives a short term projection for the use of energy. The United States and the industralized nations consume more than they produce and the OPEC nations make up most of the difference. Energy consumption in the United States is very high, reflecting the level of our technology and life style. Our total consumption for 1985 is essentially the same as for all nations with centrally-planned economies and only slightly less than for all other developed nations combined. We consume 27 percent of the world's total.

TABLE 9. *Production and consumption of energy.*

	1985		1990	
	Production	Consumption	Production	Consumption
Oil				
United States	10,234	21,522	9,756	21,841
Other industrialized nations	6,042	28,820	6,525	35,074
Centrally planned economies	15,295	13,992	16,995	15,905
Less developed countries	7,429	10,245	8,006	12,554
OPEC	39,257	3,678	48,823	4,731
Natural gas				
United States	16,731	18,575	15,920	18,344
Other industrialized nations	12,484	14,054	12,715	15,395
Centrally planned economies	18,339	17,684	20,793	20,106
Less developed countries	3,034	2,433	3,759	2,995
OPEC	5,879	3,720	8,759	5,051
Coal				
United States	1,038	964	1,166	1,085
Other industrialized nations	688	859	630	826
Centrally planned economies	2,616	2,561	2,986	2,911
Less developed countries	426	384	502	462
OPEC	5	5	7	7
Total consumption				
United States		96		103
Other industrialized nations		107		128
Centrally planned economies		98		117
Less developed countries		39		50
OPEC		12		16

Oil = thousands of barrels per day.
Natural gas = billion cubic feet per year.
Coal = million short tons per year.
Total = quadrillion Btu—includes nuclear, hydro, solar, geothermal.

Source: *Global 2000*, pp. 167–168.

An especially thought provoking statistic is this: the United States, with about 5 percent of the world's population, consumes more than twice the energy of *all* the less

FIG. 11. Tools that increase productivity. Eight plows are being pulled by a tractor. These two farm workers are doing the work of about 12 to 16 men with horse-drawn plows. Imperial Valley, California about 1905. Keystone-Mast Collection of the California Museum of Photography.

1890), C. King (1870–1880), Lord (1883), Marcy (1866), Powell (1875, 1876–1880, 1879, 1895), and Wheeler (1875–1881).

Secondary sources: R. A. Bartlett (1962), Bowles (1869), Brewer (1930), Cordasco (1968), Dobie (1941), P. W. Gates (1960, 1979), Hine (1973), Hine and Bingham (1963), Johnson (1901–1902), C. King (1872), Malin (1984), Michener (1974, 1978), Muir (1894, 1902), Pursell (1981), Richardson (1867), Riis (1890, 1892, 1900), Sandoz (1935, 1953, 1954, 1966), Shinn (1884), H. N. Smith (1950), Stone (1956), Tobey (1981), W. P. Webb (1931), and Winther (1964).

Human centered: Adams (1918), Andrist (1964), Austin (1903, 1906, 1917, 1932), Cather (1913, 1918, 1927), Ferber (1930), Garland (1917), Harte (1869), J. Kirkland (1887), London (1903), Meeker (1916), Muir (1913), Norris (1901), Rölvaag (1927), Steinbeck (1939), Twain (1872), and Wister (1902).

$$\frac{\textit{People} \times \textit{technology}}{\textit{Total resources}} = \textit{ecological problems}$$

The level of demand of human beings for resources from the environment depends on their numbers, the state of their technology, and the time scale involved. A few people living a simple life in a bountiful environment can be well supplied by that environment. When the size of the population, and hence the quantity of their demands, begin to exceed the carrying

developed nations with their 74 percent of the world's population.

How long will the fossil fuels last? No one knows and in recent decades the projections often seem to underestimate the supply. But the estimates are truly irrelevant for the long term. It will matter not one bit in the year A.D. 3000 whether we extracted the last bit of some essential non-renewable resource in A.D. 2010 or A.D. 2999. The basic moral question for our time is whether we choose to live as a "me now" generation or whether we feel an obligation to the generations to come.

The United States has known reserves of coal and natural gas (even though we import some) that should suffice for a few centuries. Our production of oil, however, is already well below consumption (Table 9). In 1977 the World Energy Conference estimated that oil reserves were about 2,100 billion barrels (31 billion for the U.S.). The estimated world consumption in 1985 is 28.6 billion. At that rate of consumption there is enough oil for 73 years. It is predicted that the curve for consumption will cross that for production between 1990 and 2000. (That, of course, is an exercise in prediction—consumption cannot exceed production.)

A recent U.S. Geological Survey analysis suggests that there may be less oil than has been assumed (Kerr, 1984). Estimates of how long the oil will last must include predictions of how much oil remains to be discovered worldwide. Considering how uncertain such estimates of the unknown must be, it is not surprising that the range is as great as from 280 to 2,415 billion barrels. The high estimates are about equal to the known reserves, mentioned above. The USGS believes that the high estimates are most dubious since, for them to be true, geologists would have to discover another mammoth pool of oil equal to that of the Middle East. Kerr's sobering conclusion for us is that "The estimated U.S. supply from undiscovered resources and demonstrated reserves is 36 years at present rates of production or 19 years in the absence of imports."

In another estimate (from *Global 2000*, p. 187), it is assumed that the world's total non-renewable energy reserves (coal, petroleum, natural gas, uranium, and shale oil) are the equivalent of about 161,241 quadrillion Btu. The world consumption in 1976 was estimated to be 250 quadrillion tons. If there is no yearly increase in the amount used, this reserve would last 645 years. With a 2 percent annual increase the reserve would last 133 years; with a 5 percent increase, only 70 years.

Minerals. In general the world has sufficient mineral resources to supply near-term demands. This does not mean that the known deposits are adequate but current experience suggests that new discoveries will take care of demands for the near future.

Nevertheless it must be obvious that the amounts of minerals in the earth's crust are not increasing so the prudent time to initiate drastic programs of conservation is now and not when the last remaining deposits are being exploited. We must adopt a policy of borrowing non-renewable mineral resources from the earth and recycling them for continual use, instead of destroying or discarding them.

Public concern for the environment

The intense public concern for our environment began in the United States in the 1960s and continues with pressures on our government to control air pollution, clean up toxic waste dumps, cease building more nuclear power plants until they can be run safely and there are adequate ways to dispose of their wastes, stop strip mining and the unnecessary damming of rivers, and protect and augment the national parks and wilderness areas.

Long before our times there were a few individuals who provided insightful analyses of what we do to the environment and the disastrous consequences of continuing the same behavior. More than a century ago George P. Marsh, lawyer, congressman, diplomat, and philologist, provided an analysis that in most respects remains accurate today (1865, pp. 39–40).

> Purely untutored humanity, it is true, interferes comparatively little with the arrangements of nature, and the

destructive agency of man becomes more and more energetic and unsparing as he advances in civilization, until the impoverishment, with which his exhaustion of the natural resources of the soil is threatening him, at last awakens him to the necessity of preserving what is left, if not of restoring what has been wantonly wasted. The wandering savage grows no cultivated vegetable, fells no forest, and extirpates no useful plant, no noxious weed . . . . But with stationary life, or rather with the pastoral state, man at once commences an almost indiscriminate warfare upon all the forms of animal and vegetable existence around him, and as he advances in civilization, he gradually eradicates or transforms every spontaneous product of the soil he occupies.

It is an interesting and not hitherto sufficiently noticed fact, that the domestication of the organic world, as far as it has yet been achieved, belongs not to the savage state, but to the earliest dawn of civilization, the conquest of inorganic nature almost as exclusively to the most advanced stages of artificial culture . . . . The popular traditions of the simpler peoples recognize a certain community of nature between man, brute animals, and even plants. (pp. 39–40)

He documented the destruction of soil in the Mediterranean world and its relation to the decline of civilization, the interrelations of organisms in the biosphere, the causes of soil erosion, and the consequences of the needless destruction of forests. All in all an extraordinary analysis and prediction—but not many listened. In 1865 some of America had been degraded but there was plenty left that was untouched and untilled, so no one needed to listen.

Almost a century later, an equally important study was that of Harrison Brown (1954), which set the stage for the huge literature we now have on this subject. Two of the participants in the symposium for which this essay is a part—Paul Ehrlich and Garrett Hardin—have been outstanding contributors. As a consequence, there is no need to survey here the host of environmental problems that concern us today. After providing a few key titles there will be suggestions for ways to present current problems in human ecology to students.

General references on environmental problems

My suggestions are: Benarde (1970), Berry (1977), Birch (1975), Boulding (1964), Bogue (1969), H. Brown (1954, 1978), H. Brown *et al.* (1957), L. Brown and E. Eckholm (1974), *L. Brown *et al.* (1984), Cantor (1967), Carson (1962), J. Carter (1984), Cipolla (1978), Cloud (1969), Commoner (1967, 1971), *Council on Environmental Quality (1983), Darling and Milton (1966), Dasman (1965, 1968*a*, 1968*b*), Detwyler (1971), *Eckholm (1976), Ehrlich (1968), P. and A. Ehrlich (1974), *Ehrlich, Ehrlich, and Holdren (1977), Forbes (1968), *Glassner (1983), *Global 2000 (1980), Heilbroner (1974), Hardin (1968, 1969, 1972, 1973, 1977, 1982), Harte and Socolow (1971), Holdren and Herrera (1971), Hunt (1974), Howe (1975), Hunter (1979), Institute of Ecology (1972), Kahn and Wiener (1967), Landsberg *et al.* (1963), Laszlo *et al.* (1977), Marsh (1865), Matthiessen (1964), Meadows *et al.* (1972), Mesarovic and Pestel (1974), Mumford (1934, 1967, 1968, 1970), Myrdal (1970), Naisbitt (1984), Nash (1982), Ogburn (1971), Osborn (1948), Passmore (1974), Peterson (1964), *Schneider and Londer (1984), Schneider and Mesirow (1976), Schumacher (1973), W. Schwartz (1969), Sewell (1977), G. Smith (1971), Stamp (1964), E. W. Stewart (1972), Udall (1963, 1968), United Nations (1982, 1983), U.S. Bureau of the Census (1975, 1984), Wagner (1971), Warren (1973), and Lynn White (1967).

The air we breathe

The first environmental problem in recent times to seriously concern the public at large has been air pollution. For generations this was purely of local concern: its destruction of life surrounding copper smelters; the pall of toxic air that blankets the steel mill towns; the chemical stench of pulp mills, and the industrial areas of

northern New Jersey and the Kanawha River valley of West Virginia.

Shortly after World War II a strange haze became noticeable in the Los Angeles Basin of California. It came to be known as smog (smoke + fog). Its origin was a mystery until the main source—automobile emissions—was documented by Haagen-Smit (1964, 1970). During the 1960s and 1970s every major city in the United States came to have its own polluted air.

Air pollution is a direct consequence of the dramatic increase in the level of technology that characterizes our time (Figs. 16–19). When we plug this increased value for technology, plus an increase in the number of people, into the numerator of our conceptual scheme:

$$\frac{\text{People} \times \text{technology}}{\text{Total resources}} = \text{ecological problems}$$

there will be an increase in ecological problems.

The combustion of fossil fuels and the production of a myriad of chemical substances leave us with a heavy load of undesirable by-products that must be disposed of—and the ambient air and the adjacent rivers have traditionally been the sinks of choice.

There has always been air pollution, even before human beings evolved. Noxious gases, such as sulfur dioxide and hydrogen sulfide, have been pouring from volcanoes and some mineral springs for eons. In fact, had all the noxious gases emitted into the atmosphere been retained, life would have ceased long ago. This did not happen because those paleopollutants were washed by rain to the earth where microorganisms and plants were able to convert them to useful ends. These purifying microorganisms and plants are still with us but the problem is that in many localities the load of pollutants is so great and diverse that the microorganisms and plants cannot handle them.

Air is a renewable resource under natural or near natural conditions because it is continuously purified by wind, rain, and organisms. In many areas today we have overloaded the system to the extent that the concentrations of noxious chemicals in the atmosphere are so great that the purifying system itself is being degraded.

Pollution has become boring

For the public at large and for our students there is a special problem in discussing pollution and other environmental concerns. The entire lives of students have been spent in an era of intense environmental concern about nuclear reactors and their wastes, about pesticides, food additives, air pollution, and toxic waste dumps. The news media are full of dire predictions that something bad is about to happen to us. Yet for most of us nothing does. People are not dying in the streets and gradually we are coming to accept pollution as part of life.

Human beings have remarkable abilities to adjust to harmful phenomena if they are chronic or seen as difficult to remedy. The same phenomenon will not be acceptable if it is of irregular occurrence. Death on the highways and death in war are good examples. We have come to accept as a fact of life the death of 50,000 Americans each year in motor vehicle accidents but we found it very difficult to accept the death of 47,217 Americans in the 18 year involvement (1961–1979) in the Viet Nam War. In World War II the total was 292,000, which was equal to only 6 years of highway carnage.

The fact that pollution is now chronic dulls our interest and concerns. My suggestion for discussing current environmental problems is not to present a catalog of horrors but to select a few highly specific problems, important at the moment, and subject them to a rigorous and dispassionate analysis. This will provide students with a framework for thinking about matters that will be of concern to their health, quality of life, and economic state for their entire lives. If the topic selected is of local importance, so much the better. As an example of what might be done, I will select the topic "acid deposition."

During the earlier discussion of the benefits and costs of the Aswan High Dam, it was suggested that it was useful to consider solutions of ecological problems from several points of view: individual *vs.* general

benefit; present *vs.* future gain; involvement of renewable *vs.* non-renewable resources; sustainable yields *vs.* exhaustion of resources. To these we will shortly add another—Hardin's metaphor of the Tragedy of the Commons.

Acid deposition

Acid deposition results from the combustion of fossil fuels in automobiles and industry, especially power plants. The two main starting substances are sulfur dioxide and oxides of nitrogen. In the atmosphere these combine with water to form sulfuric and nitric acids (aqua regia!). The usual name for this pollutant is "acid rain" but since about half of the acid comes down in the dry state and half as rain the preferred term is "acid deposition."

A few key references for this topic are: *Boyle and Boyle (1983), Crocker (1984), Hendrey (1984), Hicks (1984), Likens *et al.* (1979), Linthurst (1984), Luoma (1984), *National Research Council (1983), *Office of Technological Assessment (1984), Oppenheimer (1984), Roberts (1983*a*, 1983*b*, 1983*c*, 1984), and Teasley (1984).

The analysis of deep ice of the glaciers of Greenland and Antarctica indicate that prior to the Industrial Revolution the pH of rain was about 6 to 7.6. Today the pH of rainfall in the eastern United States ranges from 3.1 to 6.9, with an average of 4.4 (Boyle and Boyle, 1983, p. 131). Sulfur compounds are responsible for about two-thirds of the acid deposition and nitrogen compounds for the other third.

Extensive studies indicating that acid deposition is becoming a critical environmental problem started when some of the lakes in remote, non-industrial parts of Scandinavia began to "die," that is, the fish and other organisms became much less abundant or even disappeared. Some lakes became essentially lifeless. The water in these lakes, and most lakes where the rocks are granitic, contain only low concentrations of salts that act as buffers. Thus a small amount of acid deposition in such waters can cause large changes in pH. The dead lakes were quite acid and the cause was a mystery.

Eventually it was suspected that the cause was to be found in the smoke that was produced in the heavily industrialized areas of Britain and Western Europe and was carried by the prevailing winds to Scandinavia. This was a difficult hypothesis to accept, especially if one were an industrialist or governmental official of Britain or a Western European nation. How could pollutants in smoke be carried more than a thousand kilometers? Yet the hypothesis was tested in many ways and found to be true beyond all reasonable doubt.

One of the most discouraging aspects of this situation is that earlier efforts to negate the effects of pollution turned out to contribute to the cause. It was known that sulfur dioxide and oxides of nitrogen coming from local factories and power plants were damaging to green plants, buildings, and human lungs. So in an effort to solve the problem, much higher smoke stacks were built. These would carry the noxious fumes high into the air where they would be diluted and dispersed over a broad area. The acids would eventually reach the ground—presumably in such small concentrations that they could be handled by the natural cycles. This seemed to be a reasonable engineering and biological solution but, instead, it resulted in more widespread acid deposition.

Subsequently lakes in remote regions of New York and New England began to die; then the trees. What should be done? The ultimate answer must be to stop overloading the natural system to the extent that it cannot handle the pollutants. In the practical world of jobs, business, and politics, however, the answer is "We will have to balance the advantages and disadvantages of polluting." The matter becomes most complex because a course of action that is judged acceptable to a far-sighted environmentalist might not be acceptable to an industrialist who has to meet a payroll, produce dividends for the stockholders, and compete with industries here and abroad that do not have to be concerned about pollution abatement.

The Office of Technology Assessment (1984) has just released a detailed discussion of the problems of acid deposition and the implications for public policy. The study

outlines the tradeoffs of various lines of action that can be taken by the United States to solve its own problems of acid deposition and those of Canada for which we are partially responsible. This document is of exceptional value for any teacher wishing to discuss acid deposition as an example of an important problem in human ecology that must be solved. Of course it is but one item in a huge literature devoted to the subject.

The areas of greatest acid deposition (pH less than 4.2) in North America are a broad oval extending from New York to Tennessee and from New Jersey to Ohio, and a separate area of Canada east of the Great Lakes. Only somewhat less affected (pH less than 5) is the entire eastern half of the United States and southeastern Canada.

During 1980 about 27,000,000 tons of sulfur dioxide and 21,000,000 tons of nitrogen oxides were emitted in the United States. All states now pollute but, until recently, not to a degree that the natural cycles could not cleanse the air of pollutants. The major polluters are the north central states between the Allegheny Mountains and the Mississippi River. Municipal power plants are the major source of SO_2.

Since the prevailing winds are from the west, the gases from the Mid West are carried eastward to New England and southern Canada. About one third of the pollutants travel more than 500 kilometers, another third from 200 to 500 kilometers, and the final third might be considered to be local because it originates within 200 kilometers. The average distance from source to site of deposition is thought to be between 500 to 1,000 kilometers.

The OTA study estimates that about 3,000 lakes and 23,000 miles of streams are seriously threatened or almost dead (some are dead). In addition, there is serious damage to trees, crops, buildings, and probably human beings with cardiac and respiratory problems. All this adds up to a reduction in the quality of life for those living in New England and eastern Canada. It is conceivable that one can live with one's own pollution but those in eastern America must find it most aggravating to be forced to live with other people's pollution—especially when those other people say it's just too expensive to do anything about it. The OTA study points up the problem (p. 13):

> Various groups and individuals differ sharply on where the balance should be struck between protecting the environment and protecting other areas of economic well-being. There is little agreement on the intrinsic worth of resources or the equitable distribution of costs to protect those resources. Unfortunately, more accurate atmospheric transport models or a better understanding of the level of emissions required to protect sensitive resources will do little to solve such questions of value.

That last sentence recognizes one of the main arguments of those who prefer not to attempt to reduce pollution: "We really must have more scientific information before we can do the job correctly and not waste money." That is a favorite ploy of any group that prefers to do nothing. It may seem hard to argue against more information but in many situations there is a greater risk in not doing something than doing the best one can with the available information. (Very few physicians have all the pertinent data relevant to a very sick patient they may be attempting to treat, yet if they waited for all the data to come in, the patient might well have gone out—in a coffin.)

The pressures for more stringent controls of pollution have come from such notable groups as the National Commission on Air Quality, the National Governors' Association, the State and Territory Air Program Administrators, the National Academy of Sciences, the 1982 Stockholm Conference on the Acidification of the Environment, and the National Clean Air Coalition (composed of more than a dozen organizations such as the League of Women Voters, the Sierra Club, the American Lung Association, and the United Steel Workers of America). For these groups the data are sufficient to warrant more control of the pollutants.

Other influential groups hold that "further controlling emissions now may waste

money and impose unreasonable costs on industry and the public." Among them are the Business Roundtable, the U.S. Chamber of Commerce, the Department of Energy, and the U.S. Environmental Protection Agency. The last two may sound strange but Boyle and Boyle (1983) suggest that the Reagan Administration "is out to get the Clean Air Act," so its agencies could be expected to be against more controls. It surely seemed that way when Anne Gorsuch directed the EPA and it took great public pressure to get her removed and the agency back on the track of making some effort to protect the environment. Sun (1984) wrote that the report of another Committee of the National Academy of Sciences favoring more stringent controls appears to have been suppressed by the White House until after a House subcommittee was to vote on increasing controls over sulfur dioxide emissions. The vote was 10 to 9 not to demand more stringent controls—a vote that might have been different if the information and conclusions of the Academy's report had been available to the committee members. Only one of the 10 "nays" would have had to change his position. Thus, although "We must have more information before we can act," apparently it depends on what sort of information is to be made available.

In 1983 the Environmental Protection Agency proposed a modest program for reducing acid deposition but this was overruled by the White House. In March 1984 the EPA Administrator, William D. Ruckelshaus, replied that it would take President Reagan two more years to decide what to do. When Ruckelshaus was asked about the usefulness of still another special committee to study the problem, he replied, "It would be a wonderful idea if no one had done it before" (AP report March 15, 1984).

The problems of acid deposition, therefore, involve politics, international affairs, economics, corporate policy, possible tax burdens, as well as the health of human beings and the environment. It pits regions (Mid West *vs.* New England) and nations (U.S. *vs.* Canada; Western Europe *vs.* the Scandinavian nations) against one another. It is the sort of problem that teachers should analyze with their university science students but so rarely do.

The bottom line is costs and jobs. The technology is available that could reduce the quantity of pollutants that are spewed in the atmosphere to a level that the natural cycles could handle. The OTA (p. 14) study projects what the costs might be:

> Most of the proposals introduced during recent sessions of Congress would control sulfur dioxide emissions, since sulfur compounds contribute twice as much acidity to rainfall in the Eastern United States as nitrogen compounds and are more strongly implicated with a variety of adverse effects. This study estimates that the annual costs to reduce sulfur dioxide emissions in the 31 states bordering and east of the Mississippi River could range from about $1 billion (or less) for about a 10- to 20-percent reduction, to about $3 billion to $6 billion for a 35- to 45-percent reduction below 1980 emission levels by 1995.

The funds would be used mainly to upgrade older plants since they are the main polluters. More recently constructed plants have better control devices. If no action is taken it will require up to 40 years—to A.D. 2020—for the older plants to be retired. Even if action starts today, the OTA estimates that it will require a decade to reduce the emissions. During that interval there can be considerable damage to resources. The Environmental Defense Fund (1984) has this opinion:

> Current scientific understanding of acid rain strongly indicates that the Reagan Administration's "wait and see" policy may result in irreversible ecological damage.

Who should pay that $1 to $6 billion bill? Should a citizen of Arizona have to foot the bill for cleaning up the dirty air produced by a public utility company in the Mid West so that the fish in a New England lake, which that citizen will never see, can survive? If pollution affects the public at large, shouldn't the public at large pay for the remedial actions? Or a different atti-

tude might be, since the United States can hardly be blamed for the direction of the winds, why should it be held responsible for environmental damage in Canada?

In testifying against proposed legislation to reduce SO_2 emissions by 10 million tons (of the total of 27 million), Senator Byrd of West Virginia is quoted as saying that the financial impact on the industry of his state would be staggering and as many as 24,500 people would lose their jobs. What is needed, he suggested, is more research, not more controls.

So what are the specific tradeoffs? If the decision is made to reduce SO_2 emissions by about 10 million tons per year, the cost will be an estimated $3 to $6 billion.

If industry is forced to bear the costs, some old plants will probably have to close, the cost of doing business will be greater, profits might be less, the costs of the products might increase, and competition with industry that did not have to install controls (here or abroad) might be severe. Since the main target of the clean-up would be public utility plants, there would probably be an increase in the cost of electricity to consumers. This is predicted to average about 4–5 percent but in some states 10–15 percent. The greatest increases would be felt by consumers in Missouri, Indiana, Ohio, West Virginia, Pennsylvania, Georgia, and New Hampshire.

The question of jobs is important, especially for those specific individuals who lose them. Nevertheless, the overall effect of installing emission controls would be to *increase* jobs. The control devices would have to be manufactured, installed, and maintained. That $3 to $6 billion investment in emission control would mean very many more jobs.

Other job opportunities would shift. Most of the coal used in the polluting Midwest plants has large amounts of sulfur. It is mined nearby. If pollution control measures called for replacing its coal with high sulfur content with low sulfur coal from the West, the job opportunities would also move West. There is no question that pollution abatement measures would inconvenience some workers but the overall consequence would be more jobs.

We now have sufficient information to start to deal with the four points of view suggested earlier.

Individual benefit vs. *general benefit.* The balance here is for the general benefit. A large number of people would have clearer air, fewer respiratory and cardiac problems, and their homes and buildings would suffer less damage. Those who enjoy the outdoors would gain; our timber, water, and soil resources would no longer be adversely affected. There would be more work for manufacturers of control devices and job opportunities would increase. The moral question of the right of one region to degrade another would be moot. The costs would be higher utility bills (or taxes if the government paid the costs of abatement), possible disadvantages to the polluting industry, some jobs lost and the need to move elsewhere for new jobs, and a possible increase in bureaucracy.

Present vs. *future gain.* The costs of control measures, job dislocation, loss of dividends, and governmental interference would all be short-term losses. Since it would require a few years to make any significant improvement in the quality of air, the immediate benefits would be largely psychological. The truly spectacular gains would come in about a decade.

Renewable vs. *non-renewable resources.* Control measures would be of great benefit for renewable resources. Those forests, waterways, soils, and human beings previously at risk would be relieved of the acid deposition or have it reduced to more acceptable levels. The air would be able to cope better with the load of wastes. Weathering of buildings and corrosion of metals would be less. And to the extent that the human spirit is a renewable resource, there would be important gains.

Sustainable yields vs. *exhaustion of resources.* The productivity of forests, waterways, and possibly agricultural land would be increased by efficient control measures.

One cannot avoid the conclusion that the benefits of controlling the quantity of acid deposited far outweigh the costs. The many would share the benefits and a few would share costs with the benefits. That conclusion is, of course, my own. Others balance

the costs and benefits and come to different conclusions. The OTA study provides a large amount of fascinating data, only a trace of which has been touched on here, and could be the basis for some sober and important discussions with students.

The question of the rights and wrongs in this environmental matter can be greatly illuminated and clarified if we consider the implications of Garrett Hardin's (1968) classic essay, *The Tragedy of the Commons.*

The Tragedy of the Commons

In earlier times it was not unusual for villages to have grazing land set aside for the animals belonging to the inhabitants. This resource for all was known as the "commons." The inhabitants of the village would gain in relation to the number of their animals put at pasture in the commons. A rich person with 10 cows would be consuming 10 times the resources of a poor person with a single cow. This was seen as a reasonable arrangement so long as the carrying capacity of the commons was not exceeded.

But what happens when the carrying capacity has been reached and the person with 10 cows decides to graze 15? There will not be enough food for all cows and their milk production will be reduced. However the person with the 15 cows will obtain more milk than from the original 10, while the person with the single cow will obtain less. It would be to the advantage of this person to try to add another few cows.

> Therein is the tragedy. Each man is locked into a system that compels him to increase his herd without limit—in a world that is limited. Ruin is the destination toward which all men rush, each pursuing his own best interest in a society that believes in the freedom of the commons. Freedom in a commons brings ruin to all. (p. 1244)

Hardin's metaphor describes many of the frustrations, diseconomies, lessening of the quality of life, and assaults on the environment that plague us today. Acid deposition is a typical case. Historically the atmosphere has been accepted as a commons—the most important commons we have. The smoke of ages has been spewed into it but, until recently, the restorative mechanisms of nature have kept it pure. No longer.

The emissions of the power plants burning sulfur-rich coal would rapidly reach lethal concentrations were they confined to the immediate zone of their production. The solution, therefore, is to spread the noxious fumes far and wide. Thus the burden becomes shared by many in an area thousands of square kilometers in size. Many are made to suffer for the few who are unable or unwilling to cease polluting.

A steel mill that empties its wastes into the adjacent river gains by having a cheap mechanism for disposing of wastes, but all those downstream have been robbed of a common resource.

Hardin's *Tragedy of the Commons* should be required reading for all students, for Senator Byrd (whom I quoted earlier), and, if I had my way, for all human beings. It tells us a great deal about ourselves and the cause of many of our problems. It is also an excellent basis for discussions with students.

There are many tragedies of the commons in everyday life. One of the most important commons for a university is its library. If it is shared honestly and honorably it is a valuable resource for all. The tragedy comes when pages are removed for the benefit of one and the loss of all others; when books are hidden in the stacks by students who then have access to a valuable resource that is denied their classmates; when a professor's bookshelf is filled with volumes never used but not available for browsing by the library's patrons.

Littering parks and highways may be convenient for the litterer who will rarely return to see his garbage but the quality of life for all others will be lessened. The person who understates income on those 15 April tax forms gains (unless caught) whereas all others lose.

Specific topics for classroom discussion

Acid rain is but one of many specific topics relating to air that can be developed. Others are lead poisoning from leaded gasoline, asbestos and asbestosis, the role of

ozone in damaging plants and shielding us from ultraviolet, carbon dioxide and climatic change, smog and human health, tobacco smoke as it affects the smoker and those nearby, and silicosis. Ehrlich, Ehrlich, and Holdren (1977) provide introductions to the subjects and guides to the literature.

The water we drink

Actually we do not drink very much of it, yet when we read a headline to the effect that the United States is running out of water, our vision is of citizens with parched throats and lolling tongues. But that is an erroneous vision. Most of the water we use goes for our technology of farm and factory, rather than for domestic purposes.

In 1940 the total water withdrawn in the United States was 136 billion gallons per day, or 1,027 per capita gallons. By 1980 the total had grown to 450 billion gallons and the per capita gallons were 1,953 (these and other data from the U.S. Bureau of the Census *Statistical Abstract of the United States 1984*). Those 1,953 gallons per day are about 100 times the volume of an average human being.

Of the 450 billion gallons withdrawn per day, 47 percent went to steam and electric utility plants, 33 percent for irrigation, 10 percent for industry, 8 percent for public water utilities, and 1 percent for rural domestic use.

Per capita daily withdrawals showed great regional variations. Your students may wish to speculate why the per capita consumption per day was 534 gallons for the District of Columbia, 967 for New York, 2,272 for California, 5,512 for Colorado, 11,368 for Wyoming, 13,959 for Montana, and 19,007 for Idaho.

The hydrographic cycle

The hydrographic cycle describes the complete history of water in evaporation, precipitation, and movement through the earth. It accounts for the renewable-resource properties of water. Evaporation from land and sea, plus transpiration by plants, carries water into the atmosphere from which it returns as rain or snow. Part of the rain that reaches the earth runs off as streams, which enter rivers flowing to the sea, or, in some inland basins, to dry lakes or highly saline bodies of water (such as the Great Salt Lake in Utah and the Dead Sea between Jordan and Israel). Another part percolates into the soil. Some of this is used by plants and other organisms while the rest, known as groundwater, moves down to to occupy a zone of saturation. The upper edge of the groundwater zone is the water table. Groundwater moves horizontally and slightly downward until it reaches a river, lake, or the ocean. Some geological formations, such as sandstone, are highly porous and can contain large amounts of groundwater. These are known as aquifers. Most of the water on land is groundwater, which remains nearly constant from year to year and reflects the annual fluctuations in rainfall only slightly.

The hydrographic cycle of evaporation and precipitation are so finely balanced, on a worldwide basis, that not only groundwater, but also rivers, lakes, streams, seas, and oceans remain nearly constant in volume.

There are two sources of our water, surface and underground and we obtain about equal quantities from each. The surface withdrawals are from springs, streams, rivers, and lakes. This is the source we can see and it is the source that is in the greatest present danger of being degraded.

Underground water can be obtained by digging wells in most areas of the world, even desert regions. Recall the problem the early settlers of the Great Plains had in obtaining water. The scarcity of perennial supplies of surface water prevented farming until windmills became available for pumping underground water.

Although water is our most abundant renewable resource, there have always been problems with obtaining sufficient amounts. Even in areas where the rainfall is adequate for agriculture, years of drought do come. Areas of deficient rainfall, such as the Near East, much of the American West, the center of Australia, and zones in Africa both north and south of the equator have too little water (without irrigation) to allow much agriculture.

Water and waste disposal

In highly industralized and densely populated regions the basic problem with water is that demands overwhelm the ability of the hydrographic system to supply high quality water in the quantities demanded. Part of this is a consequence of our using water for the disposal of wastes from homes and factories. Human wastes and liquid wastes enter the sewers and go to the treatment plants. (Other wastes are solid and are trucked away to the city dump or landfill yet, we will see that they, too, can pollute water.)

A few generations ago it was customary for towns and cities to empty their raw sewage into nearby streams or, in the case of New York City, into the Hudson River, which then emptied almost immediately into the Atlantic Ocean. Therefore it is an improvement today to have sewage treatment plants. The job they do depends on the type of plant. In Primary Treatment plants the solid wastes and part of the particulates are screened out and chlorine is added to kill some of the microorganisms. The partially purified water then is dumped into a river, lake, or the ocean. About 29 percent of the treatment plants in the United States are of this sort.

Another 67 percent provide Secondary Treatment for the sewage. Chlorine is not added and the microorganisms are allowed to act on the organic wastes—in a real sense this is what would happen under natural conditions. That is, if only a moderate amount of sewage consisting mostly of human wastes is emptied into a river, the bacteria, protozoans, and other organisms will feast and convert the wastes into themselves. This is the carbon and nitrogen cycles in action. (The old rule of thumb was that a river cleaned itself in ten miles.)

About 3 percent of the plants use a much more complex Tertiary Treatment. This removes nearly all of the organic wastes and leaves water that can be used for irrigation and nearly all purposes other than human consumption (even that stage may be reached in the near future).

The organisms that break down human and similar organic wastes have been selected over the millennia for using such materials as food. Modern industry, however, has its own incredible list of wastes. Some of these are highly toxic to all organisms, including those upon which we have traditionally relied for consuming human and domestic wastes. Thus, when organic solvents, heavy metal salts, pesticides, and a host of other chemicals are dumped into the sewers, they lessen or even abolish the ability of the microorganisms to handle the familiar wastes.

Additional types of wastes that pollute waterways are a consequence of agriculture and mining. It is not unusual for American farmers to add much more fertilizer than is required for optimal yields. They also use a large variety of toxic chemicals to control insects and weeds. These materials can wash into waterways and cause serious pollution problems. The waste-water from mining operations is usually highly toxic.

Water pollution

The Council on Environmental Quality (1983) is guardedly optimistic in suggesting that water quality may be improving. (The CEQ is appointed by the President and, among its other duties, prepares his annual report to the Congress on *Environmental Quality*. The report tends to emphasize the positive.) Most improvements are the results of federal legislation such as the Clean Water Act, the Safe Drinking Water Act, and others. However, the conventional tests measure the old fashioned sorts of wastes, not the new technological wastes. These are of great concern but there are indications that they may be decreasing in quantity. For example, in those industries that have installed the BPT (Best Practical Treatment) technology, suspended solids, oil and grease, dissolved solids, phosphate, and heavy metals were reduced by 52 to 80 percent between 1972 and 1982.

One interesting biologial test of water quality is to sample the fish populations. Although water quality has not deteriorated in the last five years, about 56 percent of the nation's waters still have a damaging effect on fish populations. Turbidity,

nutrient surpluses, toxic chemicals, and low oxygen are the main factors. The sources of pollution can be point (municipal and industrial discharges) and nonpoint (mainly agricultural runoff). The point sources give problems in 20 percent of the streams and agricultural runoff in 29 percent, with 17 percent being badly polluted.

The CEQ 1983 report concludes:

> The nation's waters are generally moving toward the Clean Water Act goal of achieving fishable and swimmable waters. Although the nation's waters are still affected by pollution problems from both point and nonpoint sources, a number of once polluted streams, rivers, and lakes now support viable fish populations.

That is all to the good, but apparently many formerly nonpolluted waters are now polluted.

Here we have another Tragedy of the Commons. Water, like air, was viewed as a "free" resource that could be used in any manner desired. This attitude is changing and, in spite of the varied signals that come from Washington, it is probable that the nation's waters will slowly improve.

Water for the future

The long-term problem with water is more likely to be the lack of quantity rather than quality. The *Global 2000* (p. 344) prediction for the world is:

> Freshwater, once an abundant resource in most parts of the world, will become increasingly scarce in coming decades for two reasons. First, there will be greater net consumption, by cooling towers and, especially, by irrigation so that the total supply will decline. Second, pollution and the impacts of hydraulic works will effectively limit the uses of freshwater—and therefore, in effect, the supply. The deterioration of river basin catchments, especially as a result of deforestation, will increase the variability of supply, accelerate erosion, damage water development projects, and degrade water quality. It seems inevitable that the function of streams and rivers as habitat for aquatic life will steadily be sacrificed to the diversion of water for irrigation, for human consumption, and for power production, particularly in the LDCs.

This is just one more example of the consequences of overwhelming the cycles that provide renewable resources. As usual the problems for the LDCs are more serious:

> The lack of safe water supplies and methods for sanitary disposal of human wastes and waste water means that as many as 1.5 billion persons are exposed to fecally related disease pathogens in drinking water. These problems of water supply and quality in LDCs are so severe as to be matters of survival for millions of persons.

To put this problem in a human perspective it is well to note that 1.5 billion is seven times the population of the United States. And what about us?

> In industrial nations, water supply and quality will pose more subtle and therefore more complex questions of tradeoffs and conflicts among users (or values) of freshwater. Water resources management in such nations is concerned not with human survival but with balancing demands for water resources against considerations of quality-of-life. But scarcities and conflicts are becoming more acute, and by the year 2000 economic, if not human, survival in many industrial regions may hinge upon water quality, or water supply, or both.

It was mentioned earlier that most of our water resources are groundwater, which supplies about half of our withdrawals. The CEQ 1983 *Annual Report* estimates that the United States has between 30,000 and 60,000 trillion gallons of groundwater of which 15,000 trillion are practical to withdraw. However only about 400 trillion gallons are in situations where replenishment occurs. The reason: "once depleted, most ground water cannot be recharged readily or practically, because it has accumulated over geologic time" (p. 86). Thus of the total readily available, 14,600 trillion gal-

lons are a non-renewable resource and only 400 trillion can be considered renewable.

Groundwater is of special importance in the arid west where its use in irrigation provides a rich agricultural return. In large areas, however, the groundwater is being removed far more rapidly than it is being replenished by rain. The "overdrafts," that is, the excess removed, are especially serious in much of Kansas, Oklahoma, Texas, Arizona and parts of California, Nebraska, and New Mexico. The overdrafts in 1980 in these areas were 12.4 billion gallons per day.

Sheridan (1981, p. 122) makes this prediction:

> On the High Plains of Texas, crop production is expected to decline between 1985 and 2000 because of the depletion of the Ogallala Aquifer. And, certainly, the end is in sight for irrigation-dependent increased grain yields from western Kansas and Nebraska as their water tables continue to drop.

Contamination of groundwater

There will be more and more reports during the next decade of the contamination of groundwaters, especially those secret stores, the aquifers. Seepage from toxic waste dumps, which have increased so dramatically since World War II, is entering some aquifers. It would be interesting to have your class suggest how one might prevent contamination of the aquifer from a nearby toxic waste dump and, if it occurred, how the aquifer might be cleansed. According to Pye, Patrick, and Quarles (1983, p. 8), "remedial action is complex, time-consuming, and extremely expensive" and "often it is more cost-effective to locate a new source of water than to attempt treatment."

"Foul and Flee"—that has been our *modus operandi* wherever and whenever it was (or is) possible and in the vast and resource-rich United States this was usually possible. Now we are entering an age, which will last forever, when we must learn to live with what we have.

So it appears that the projections are for a large increase in the numerator of our model:

$$\frac{\text{People} \times \text{technology}}{\text{Total resources}} = \text{ecological problems}$$

That is, although the projections are for a slow growth in population size, the level of technology will increase greatly—and so demand very much more water. Yet the denominator, our total water resources, will remain much the same. The increase in ecological problems, therefore, is inevitable. That is, unless we plan to live as partners in this world rather than at its expense. Living at its expense is solely a short-term option.

Specific topics for classroom discussion

1. Every community in the land has problems with water. One interesting case history might be a study of the source of the local water supply, how it is used, how it is treated after being used, and the condition of the place where it is disposed. A good reference to start this or any study of environmental problems is Ehrlich, Ehrlich, and Holdren (1977; the main discussion of water will be found on pp. 257–272, 556–561). Other references: Blake (1956), Burby *et al.* (1983), Camp (1963), Council on Environmental Quality (1974, 1983), Environmental Protection Agency (1977), Hirshleifer *et al.* (1969), L. B. Leopold and Davis (1966), Luken and Pechan (1977), Powledge (1982), U.S. Department of Agriculture (1955), and Zwick and Benstock (1971).

2. For the special case of groundwater contamination see Pye, Patrick, and Quarles (1983) and Geophysics Research Forum (1984).

3. Toxic waste dumps have been much in the news for the past few years and they are an extremely difficult environmental problem. The United States is pitted with thousands of toxic chemical time bombs. The vast expansion of technology in the decades since World War II has seen the production of huge quantities of toxic by-products of industry. Until quite recently very little attention was paid to proper disposal. The solution was usually to empty

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the stuff in a pit and hope for the best. In many instances public health authorities are unaware of the existence of such dumps. The Love Canal episode has been national news. Today my car radio announced that 60 wells used by the Los Angeles water district have been found to be contaminated by organic solvents and must be closed.

The quantities of solid wastes produced is prodigious. *Statistical Abstract* gives a total of 146 million tons for 1981. The major contributors were the chemical industry with 30 percent and the primary metals industry with 25 percent.

Material from a toxic waste dump slowly seeps into the ground and, if that were the end of it, fine. But more often than not the toxic chemicals reach the groundwater and it then becomes almost impossible to prevent their spread.

For references see those given for topic 1 above and also K. W. Brown, G. B. Evans, and B. T. Frentrup (1983), Francis and Auerbach (1983), LaGrega and Hendrian (1983), Lester and Bowman (1983), and Toxic Substances Strategy Committee (1980).

4. In the arid west water is gold—and seemingly it is sought as eagerly and as deviously. A classic and well-documented case of grabbing water concerns Los Angeles and the Owens Valley. In the early 20th century the city of Los Angeles acquired the rights to essentially all of the water in the Owens Valley—a wild and wonderful area to the east of the Sierra Nevada. It was a bitterly contested move but in the end money and strong-arm persuasion got the water for Los Angeles. Two aqueducts were built, each about 400 kilometers in length. It was an extraordinary engineering achievement. Having lost its water Owens Valley slowly became a near desert. Mary Austin (1903) in her *Land of Little Rain* described the original beauty of the Owens Valley.

The bitterness remains to this day and, currently, is centered on the preservation of Mono Lake. This is a highly saline body of water with a rich and interesting biota. Los Angeles has the rights to the streams that enter Mono Lake (Mark Twain's *Roughing It* country) and has diverted much of the water. The level of the lake has dropped, endangering this unique piece of nature.

A century ago John Wesley Powell (1879) provided a blueprint for the wise allocation of water in arid lands that had insufficient supplies. The sordid politics associated with the Owens River project shows the intensity of struggles for scarce resources. Kahrl (1982) has provided a splendid account of the Owens Valley Project. See also Kahrl *et al.* (1979), Hoffman (1981), and Ostrom (1953).

For more general treatments of competition for resources see Hays (1959) and and Blake (1956).

5. A more general problem relating to water resources is desertification. Long ago Paul Sears (1980, now updated) wrote a classic treatment, *Deserts on the March*, which showed clearly that at least one of the drummers was mankind. A recent study by Sheridan (1981, pp. 121–122) reaches these conclusions:

> Desertification in the arid United States is flagrant. Groundwater supplies beneath vast stretches of land are dropping precipitously. Whole river systems have dried up; others are choked with sediment washed from denuded land. Hundreds of thousands of acres of previously irrigated crop land have been abandoned to wind or weeds. Salts are building up steadily in some of the nation's most productive irrigated soils. Several million acres of natural grassland are, as a result of cultivation or overgrazing, eroding at unnaturally high rates. Soils from the Great Plains are ending up in the Atlantic Ocean.
>
> All total, about 225 million acres of land in the United States are undergoing severe desertification—an area roughly the size of the 13 original states.
>
> The federal government subsidizes both the exploitation and conservation of arid land resources. But the subsidies for conservation are meager compared with those for exploitation. Low interest

> government loans for the installation of irrigation systems encourage farmers to mine groundwater . . . . Federal disaster relief and commodity programs encourage arid land farmers to plow up natural grasslands to plant crops such as wheat and, especially, cotton. Federal grazing fees that are well below the free market price encourage overgrazing of the commons [Sheridan must have read Hardin!].
>
> Federal subsidies are, in other words, a major force behind the desertification of the United States.

These quotes are not from a wild-eyed environmentalist group but from a publication of the President's Council on Environmental Quality.

It is absolutely necessary for university students today to understand these problems of human ecology that involve biology, geology, politics, economics, tradition, and the way people balance short-term and long-term goals to the detriment of the latter ("me-nowness"). It is important because, in this example, desertification results in "the impoverishment of ecosystems as evidenced in reduced biological productivity and accelerated deterioration of soils and in an associated impoverishment of dependent human livelihood systems" (Sheridan, p. iii).

The food we eat

American agriculture continues to be one of the success stories of our time. In spite of problems that would seem to render it ineffectual, it continues to provide ample food for consumption at home and produce a surplus on which many other nations have come to depend.

Productivity of United States agriculture

Data were given earlier that indicate the great increase in yields per acre and the decrease in the labor required to produce crops. Here is another example (nearly all of these data are from *Statistical Abstract*, 1984). Corn is our most valuable crop. In 1981 it was worth $19 billion. In the 1961–1965 period the average yield per acre was 66 bushels and it required 11 man hours to raise 100 bushels. In 1981 the yield had increased to 110 bushels and the time required had dropped to 3 man hours.

TABLE 10. *The United States role in world agriculture.*

	U.S. production as a percentage of world production	Percentage of U.S. production exported	U.S. exports as a percentage of world exports
Wheat	16.9	63.3	48.1
Corn	47.5	24.0	70.4
Soybeans	63.0	46.5	86.6
Rice	2.0	—	21.6
Tallow	52.7	—	56.3
Tobacco	15.8	34.4	17.8
Vegetable oils	14.6	—	9.6
Cotton	23.1	42.3	32.2

Source: U.S. Bureau of the Census. 1984. *Statistical Abstract.* Tables 1190 and 1191.

The increased productivity of soil and labor has come from improved techniques that have changed traditional agriculture from a natural enterprise that was labor intensive to a programmed and mechanized branch of technology: the value for farm equipment was $23 billion in 1960 and $109 billion in 1981; the total amount of fertilizer used for crops in 1960 was 25 million tons; in 1981 it was 54 million tons.

International importance of United States agriculture

In 1982 the total number of farm *workers* was 4,108,000 or 1.8 percent of the total population of the nation (and 3.1 percent of all workers). The United States farm workers account for 0.1 percent of the world's total population yet, they produce 63 percent of the world's soybeans of which 47 percent is exported. The amount exported is 87 percent of the world's trade in this vital crop (Table 10). The other data of this table show the astonishing productivity of that 0.1 percent of the people of the world.

Prognosis for farm productivity

All projections indicate that in the next few decades there will be a large increase in the world's population, that most nations will become net importers of food, and that agricultural lands throughout the world will

be degraded. Vast amounts of food will be required to feed the added multitudes and the United States will be the principal producer of surplus food that can be exported. The prognosis for the state of agriculture in the United States during the next few decades, is therefore, of worldwide concern. The following information is based mainly on Batie and Healy (1980, 1983), Council on Environmental Quality (1983), and *Statistical Abstract* (1984).

The mildly optimistic answer is that the United States can continue to meet export needs for the near future. However, these goals will be met only by a continuing degradation of the land's productivity. These are some of the problems.

Land availability. Of the nation's 2.2 billion acres of land, 1,359 million acres are suitable for agriculture. Of this 413 million acres (30 percent) are crop land; 414 million acres (30 percent) are range land for grazing animals; 376 million acres are in forest (28 percent; much of this is farm land that has been abandoned to trees); and 153 million acres (11 percent) are not available for agriculture (mining, industry, homes, freeways, etc.). About 5 percent of the crop land is irrigated.

If additional land is required in the future, as it surely will be, there is a reserve in the eastern states of the former farm land that has reverted to forest. This is not the best land, by U.S. standards, and much of it was abandoned long ago when more productive lands of the Midwest became available.

Development. An estimated 875,000 acres are withdrawn each year for urban use. Historically this usually has been the better agricultural land. The early settler-farmers selected the best land available and, as they prospered, this land became the sites for towns and later cities. For example, in the southeastern states 15 percent of the prime agricultural land had been converted to other kinds of development. Conversion is 10 percent in the northeast states.

Mining activities are expected to require about 568,000 acres at any one time until the year 2000. That portion subject to strip mining operations may not achieve its original fertility once mining has ceased.

Salinization. About one third of the irrigated crop lands in the West now have excessive levels of salt and the problem is expected to increase, resulting in reduced productivity or loss as crop land.

Reduced water for irrigation. In the section on water, it was mentioned that the huge Ogallala Aquifer, and other sources of groundwater, are subject to serious overdrafts for irrigation. Hence, the same land will not be able to produce as abundantly when irrigation water becomes less available.

Wetlands. These are of great importance for the general ecology of the regions where they occur and indirectly for agricultural land. They are being eliminated at the rate of 450,000 acres per year.

Desertification. Mention was made earlier of Sheridan's (1981) estimate that 225 million acres in the United States are now undergoing severe desertification.

Erosion. The Department of Agriculture has estimated that one third of our cropland is eroding at a rate that will decrease productivity. The average loss of topsoil per acre per year is 4.7 tons. This is regarded as a tolerable limit since natural forces can regenerate the land to that extent. Since that is the average, it means that half of the land is eroding at above the acceptable level. A recent news report quoted an expert of the U.S. Department of Agriculture as estimating that topsoil from about 100 million acres is washing away faster than it is being replaced and that about 8 percent of crop land is so highly erosive that further erosion cannot be prevented. Erosion by water is a problem mainly for the eastern states and those in the Mississippi Valley. Wind erosion is most severe in Texas, New Mexico, and Colorado but it is also a problem in all of the other states of the High Plains.

Different authorities will reach their own conclusions about the extent to which we are over-using our agricultural lands. The more optimistic seem to think that real problems will not appear until the turn of the century. The essential fact, however, is that no rate of degradation can be sustained and, it would appear, our abuse of agricultural land is substantial.

The only long-term solution is to undertake curative actions for the land already abused and to use land in such a way that its productivity is not decreased. There really is no viable alternative.

Liebig (1841, p. 141) reminds us of what we started with:

> The first colonists of Virginia found a country, the soil of which was similar to that mentioned above [an extremely rich soil]; harvests of wheat and tobacco were obtained for a century from one and the same field without the aid of manure, but now whole districts are converted into unfruitful pasture land, which without manure produces neither wheat nor tobacco .... Almost all the cultivated land in Europe is in this condition.

The one happy aspect of this otherwise menacing situation is that the scientific and practical information is available to allow land to be used in a non-destructive manner. The transition from destructive to non-destructive agriculture, however, will be an extremely complex matter involving national policy, competing business interests, cost of living, life styles, balance of payments in international trade, and emotionally difficult decisions on the extent to which we can help to feed the hungry people of this world.

References

Start with Ehrlich, Ehrlich, and Holdren (1977, pp. 247–257, 283–285, 561–567). J. R. Anderson (1970), *Batie and Healy (1980, 1983), Berry (1977), Borgstrom (1968), H. Brown (1954), L. Brown (1970, 1978, 1984), L. Brown and E. Eckholm (1974), Carson (1962), Conning and Landsdown (1983), Council on Environmental Quality (1983), Committee for the World Atlas for Agriculture (1969), Crosson and Frederick (1977), Duckham, Jones, and Roberts (1976), *Eckholm (1976), Eyre (1963), Fussell (1976), Glassner (1983), *Global 2000 (1980), Gras (1940), *Halcrow (1977, 1980, 1984), Howe (1975), Hinman (1984), Knutson, Penn, and Boehm (1983), Paarlberg (1980), *Pimentel *et al.* (1982), Rasmussen (1982), Scientific American (1971, 1973), Sewell (1977), Symons (1979), Turner (1970), Vicker (1975), and the entire 9 May 1975 issue of *Science*.

Specific topics for classroom discussion

Possibly the most important, though most difficult (for the teacher) and most frustrating (for the students), topic to develop with a class would be to formulate an agricultural policy for the United States. The references just given, especially those starred, will provide background information. Here are some Socratic ploys that could be used to stimulate students to think deeply about a network of problems that are as important as one can imagine.

1. Is the nation exporting its future welfare when, in order to produce a large surplus of food to be shipped overseas, it uses soil and water at a rate greater than they can be replenished?

But we must continue to export food because the dollars earned are needed to pay for imported oil.

And there is a moral obligation to try to help those in the world who need help. We must be our brother's keeper.

But our resources are finite and we cannot hope or be expected to keep an infinite number of brothers.

2. America's high technology agriculture now uses from two to six times (depending on the crop) as much caloric energy to produce food as the food contains. Will not the Second Law of Thermodynamics put an end to that? ("Yes" to the degree that non-renewable resources are used for energy; "no" to the degree that renewable resources are used for energy.)

3. Yields of food have been greatly increased by the use of antibiotics in animal food and by the use of pesticides. This means more food and possibly larger profits for the farmer and lower costs for consumers. However there are problems.

About half of the antibiotics produced in the U.S. go into feed for animals. It has long been feared that pathogenic organisms in the animals might develop resistant strains and, should they reach human beings and cause disease, the usual treatment with antibiotics might not be effec-

tive. Holmberg *et al.* (1984) have shown that this is happening. How should one balance the interests: greater profits and possibly less expensive meat *vs.* the health of the public?

Pesticides control the pests of crops and in this way are of great benefit. However, residues on food and exposure of agricultural workers to the pesticides are potentially hazardous. In addition, the pests often evolve resistant races and, in order to control them, higher doses or different pesticides must be used. How should these benefits and risks be adjudicated?

4. Wind erosion is often caused by plowing land where marginal amounts of rain occur and planting it with grain. When the drought years come the soil is blown away. That was the cause of the Dust Bowl of the 1930s. It is to the advantage of the farmer to try to raise a crop, if prices are high, and it is to the advantage of the nation at large that the land not be degraded. Should the owner of the land have full control over how it is used? Should the government regulate the use of land?

5. Faulty irrigation methods continue to cause the salinization of rich farm land—just as it did for the early farmers in Sumeria. What is the solution?

6. The Federal Government has a long standing policy of price supports for farm products, of purchasing surplus food, or of paying farmers not to grow crops. These programs are to remedy overproduction. Is there a better system?

7. And the overall question is: Can we afford those agricultural practices that are geared for profits now but losses later?

One can keep this list current by keeping up with the news and encouraging the students to do so.

Special topics III

Topics that might be the basis for short oral reports by students for Part III come from the important issues of the day. Current issues of daily newspapers, weekly news magazines, the "News and Comment" section of *Science, BioScience, Audubon* and the other environmentally oriented journals will include more up-to-date possibilities than the following references.

Environmental protection in the Third World. Balancing short-term and long-term needs. See E. Eckholm (1982).

Killing our national parks. That is what "improvement" often does. See J. L. Sax (1982).

The future of American agriculture. It will depend on land, water, energy, and worldwide demand. See S. Batie and R. Healy (1983).

Is the sea to be a commons? International rules are being proposed. See E. M. Borgese (1983).

Phosphate rock. It is important for fertilizer. See R. P. Sheldon (1982).

Sunflowers. They are an important source of oil. See B. H. Beard (1981).

Diseases old and new. Some of our current ones may be new; others that appear to be new are likely to be altered old ones. See E. D. Kilbourne (1983).

Plastic pollution of the sea. It is a growing problem for the animals. See D. H. S. Wehle and F. C. Colman (1983).

The Amazonian rain forest. The greatest forest on earth is being destroyed rapidly. See C. Uhl (1983).

Elephant seals. After being slaughtered down to a population of about 100, they are making a dramatic recovery. See G. F. Carroll (1982).

Acid rain in New England. It's killing the forests. See H. W. Vogelmann (1982).

Pelicans as pollution monitors. Almost eliminated by pesticides, they are making a come-back. See R. W. Schreiber (1982).

Harnessing the Colorado River. Dams are changing the ecology of the area. See S. W. Carothers and R. Dolan (1982).

New light for the future. There will be a gradual shift to renewable sources of energy. See L. R. Brown (1982).

Pollution and resistance to disease. Our immune systems are being affected. See L. D. Caren (1981).

The Army Corps of Engineers vs. *the environment.* Another major battle in this chronic war. This time some wild areas of Florida are in jeopardy. See G. Martanto (1984).

Deadly incident in Juarez. A radiation spill that could be the world's worst so far. See M. Kevin (1984).

The second Green Revolution? Genetic engineering may greatly increase the food supply. See S. Siwolop (1983).

International migrations. Human beings are undertaking the greatest mass movement in history to obtain more resources and seek a more secure life. See L. F. Bouvier (1983) and C. V. Carnegie (1983).

An evaluation of the human species. As we relate to nature. See M. Cartmill (1983).

Killer bees. They are headed for us from Central America and one estimate of the damage they might do to our crops is $20 billion per year. They can mount mass attacks and kill human beings. See T. Boddé (1982).

Acid smog. Fog + California smog is more acid than acid rain. And we breathe the stuff. See L. Roberts (1982).

Water for food and energy. Unless we plan carefully there will not be enough in the western states. See D. Pimentel *et al.* (1982).

Breast feeding. An efficient means of population control. See R. V. Short (1984).

Waterpower. Before the Industrial Revolution it was a major source of energy. See T. S. Reynolds (1984).

Fish for the people or power for the people? The Battle of the Hudson pitted environmentalists and public utilities. See L. W. Barnthouse *et al.* (1984).

But is it good to drink? Maybe, but we must take greater care to protect our groundwater. See L. Tangley (1984).

The costs of destroying species and ecosystems. In our increasing efforts to change the world to suit our immediate needs, many species and natural areas are being destroyed. Does it matter? "Yes" say P. R. Ehrlich and H. A. Mooney (1983).

Acid rain and German forests. It's killing them. See L. Roberts (1983*a*).

Is the U.S. killing Canadian lakes and forests? It seems to be, along with its own. How should such international disputes be adjudicated? See L. R. Roberts (1983*b* and 1983*c*).

The no-till solution for better crops. New and effective ways to prevent destructive erosion of soils. See C. Elfring (1983).

Shellfish can be desirable though dangerous food. But the Feds are trying to keep the creatures clean. See E. P. Larkin and D. A. Hunt (1982).

The "Silent Spring" revisited. More and more is being learned about the effects of pesticides on ecosystems. See D. Pimentel and C. A. Edwards (1982).

Why are the forests of the eastern United States ailing? A decline in growth began shortly after 1955 and it coincides with a large increase in air pollution. See L. Roberts (1984).

Bioeconomics of the ocean. It contains valuable food but there are few national or international rules to make it a sustainable resource. See C. W. Clark (1981).

Wood for the fire. As supplies of nonrenewable fuels decline, renewable firewood is increasing in importance. See S. Walton (1981*c*).

The environmental tradeoffs of a nuclear reactor. The increase in water temperature has pronounced ecological consequences. See J. W. Gibbons and R. R. Sharitz (1981).

Can (shall?) Chesapeake Bay be saved? Not as long as it is regarded as a "commons." See S. Walton (1981*d*).

Pure food for children. Their small size and greater susceptibility to toxic substances mean that standards for adults do not protect them adequately. See H. Babich and D. L. Davis (1981).

The overuse of water. Water should be a renewable resource but we are exceeding the rate of its renewal. See T. Boddé (1981).

IT'S TIME TO TAKE A STAND

Few, if any, of the readers of this essay will be startled by my survey of the *problématique humaine.* The seriousness of human and environmental problems is well known and there is a general feeling that the human species will move in an inexorable manner to whatever planless future is in store. I believe such a point of view lacks both courage and an appreciation of the enormous power of human beings. If our world goes to the dogs, it will be for want of will, not for want of knowledge and power.

We tend to forget that we can accomplish incredible tasks once we have decided to do them. President Kennedy told sci-

entists and engineers to put a man on the moon by the end of the decade—and they did. American agriculture is steadily increasing its ability to provide food. The variety and safety of food in the supermarkets are the best in history. New technology has revolutionized communication, transportation, construction, and personal comfort. We have come to expect miracles from the medical profession and in the few cases when they fail, we become litigious.

Although it may not be obvious to many people living in the less developed nations, there has been a gradual improvement in the human condition in the last century. To be sure, the per capita GNP for the world as a whole in 1975 was only $1,500 and for the LDCs only $380 (data from *Global 2000*). Nevertheless there is no lack of knowledge and ability to better the lives of a substantial portion of the human population.

But there are two BIG IFs . . . .

IF I

IF there is to be a desirable future, we must accept that the human experiment is worth a future. There must be an appreciation of the incredible drama of human history for the past million years or more and the equally incredible future that is possible. We have the knowledge and power to provide every human being the opportunity to lead a dignified and meaningful life, with adequate food, clothing, housing, medical services, education, and recreation. The achievement of this goal will require that we emphasize the benefits for the many above the benefits for the few.

No one suggests that this vision of a new world will be easy to achieve. It will require extraordinary changes in the way we view ourselves and the world. Take for example the dominating terror of our times—the threat of nuclear war. We require no new scientific or other information before we can forego nuclear war. Human fears and attitudes are the problem.

But there are innumerable examples of human-oriented triumphs. We have developed an agricultural system of great productivity; our technology can gratify our slightest whim; we can solve most medical problems; we have the technology to stop nearly all forms of pollution.

It is a matter of will, not way.

IF II

And there can be an acceptable future only IF we live according to the constraints of nature.

There is general agreement that the future of humanity is clouded by the fact that there are too many people and a level of technology too high for the environment to long sustain. We are now living beyond the environment's means or, we might say, are living not only on nature's interest but also on nature's capital.

This is a perfectly feasible thing to do if we ignore IF I and decide that the future of humanity is of no concern to us. Such a point of view appears to have been held by ex-Secretary of the Interior, James G. Watt, who implied that there is no need to conserve for the future, since Christ's Millennium would soon arrive.

But if one does not ascribe to millenarianism there remains the problem of a predicted imbalance of resources and people. A basic fact, and one for great concern, is that in order to fill present resource needs, we are mining the biosphere, not cropping it. That is, we are using up non-renewable resources at an appalling rate and so overtaxing the systems that produce the renewable resources that the systems themselves are being degraded. This means that the world is becoming less and less able to support human beings.

The question of numbers of people is highly emotional. Some governments (until recently) and some religions (still) feel that the more people the better. Others view such a philosophy as committing humanity to a future of unparalleled misery and want—the Malthusian trap finally sprung.

Excluding a notable recent example, most responsible leaders of church and state understand that the world's population must be controlled. There are two main opinions as to how this is to be achieved. One group feels that the problem will solve itself since, as those nations with the high

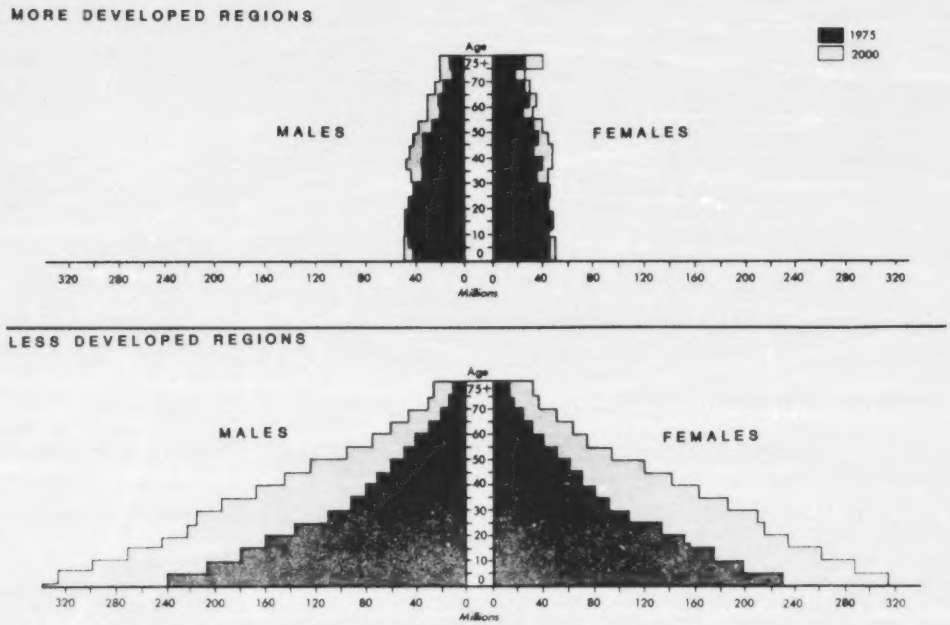

FIG. 20. Profiles of the world's population of human beings in 1975 and projections for 2000. Modified from *Global 2000*, figure 2-2.

growth rates become more prosperous, the familiar demographic transition will occur and their annual growth rate will approach zero. Thus morality dictates that we make every effort to care for every human being now alive, or about to be born, even if this results in an intolerable assault on the environment.

The second point of view holds that we must initiate population control programs on a worldwide basis and at the same time drastically alter the way we use renewable and non-renewable resources. The fossil fuels must be made to last as long as possible; the metals forever. The renewable resources—soil, air, water, plants, animals—must be cropped in an environmentally-sound manner so that their productivity is not decreased. It should be possible even to increase the productivity of the resource base by restorative actions.

I believe the first point of view is unacceptable and that the only viable alternative for a human future is that we limit the size of our population to the degree that the environment is capable of supporting human life on a sustainable basis and with an agreed upon life style. And it will make a very great difference for the quality of life whether Zero Population Growth is achieved for 4 billion, 16 billion, or 40 billion human beings.

It will be extremely difficult to achieve this goal because the people who will make the problem almost insolvable have already been born. Figure 20 (from *Global 2000*, p. 17) says much about the *problématique humaine*. The upper portion shows the age-sex composition for the populations of the developed countries. All of the age cohorts are about the same size and are predicted to remain so until 2000.

In the less developed countries, however, the largest cohorts are the young. When they reach the age of reproduction, these very large numbers of human beings will be producing very large numbers of babies. The environment cannot long support a population of the type shown in the lower half of the figure.

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If we accept IF I, that it is important for the human drama to continue, there seems no alternative but to move rapidly to adjust the population size and technology behavior of human beings to the ability of the environment to sustain us. We oversimplify our problems only slightly when we say that the less developed countries must bridle their populations and the developed countries must bridle their destructive technology.

It is highly unlikely that the world can continue "as is" in the hope that it will all work out in the end. If there is to be a satisfactory future, there must be careful, compassionate, and courageous planning now. And we must not lose sight of the fact that compassion cannot allow us to ignore the laws of nature.

Educators must take a stand

The view is often expressed that the seeds for our own destruction have already been sown. That may be so, but I cannot accept that as a reason for inaction. The view is also expressed that individual human beings can do little. That also may be statistically true but neither can it be a reason for inaction.

Those of us who teach in the institutions of higher education are neither few nor powerless. There are many of us and our power could be effective. The future leaders in all walks of life come through our classrooms and if we are able to impart a feeling of hope and an understanding of the power that is in the hands of human beings, the future that we so desire could be achieved.

It is time for us to take a stand. The Agricultural Revolution, Industrial Revolution, and Technological Revolution could be followed in our time by a Humane Revolution.

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